

CHARACTER DISPLACEMENT AS THE “BEST OF A BAD SITUATION”: FITNESS TRADE-OFFS RESULTING FROM SELECTION TO MINIMIZE RESOURCE AND MATE COMPETITION

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Abstract.—Character displacement has long been considered a major cause of adaptive diversification. When species compete for resources or mates, character displacement minimizes competition by promoting divergence in phenotypes associated with resource use (ecological character displacement) or mate attraction (reproductive character displacement). In this study, we investigated whether character displacement can also have pleiotropic effects that lead to fitness trade-offs between the benefits of avoiding competition and costs accrued in other fitness components. We show that both reproductive and ecological character displacement have caused spadefoot toads to evolve smaller body size in the presence of a heterospecific competitor. Although this shift in size likely arose as a by-product of character displacement acting to promote divergence between species in mating behavior and larval development, it concomitantly reduces offspring survival, female fecundity, and sexual selection on males. Thus, character displacement may represent the “best of a bad situation” in that it lessens competition, but at a cost. Individuals in sympatry with the displaced phenotype will have higher fitness than those without the displaced trait because they experience reduced competition, but they may have reduced fitness relative to individuals in allopatry. Such a fitness trade-off can limit the conditions under which character displacement evolves and may even increase the risk of “Darwinian extinction” in sympatric populations. Consequently, character displacement may not always promote diversification in the manner that is often expected.

Key words.—Body size, Darwinian extinction, ecological character displacement, mate choice, phenotypic plasticity, reproductive character displacement, sexual dimorphism.

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When species compete for resources or interfere with each other’s ability to identify conspecific mates, selection should favor divergent phenotypes that minimize such interactions (Darwin 1859; Lack 1947; Brown and Wilson 1956; MacArthur and Levins 1964; Grant 1972; Crozier 1974; Slatkin 1980; Taper and Case 1992; Howard 1993; Losos 2000; Schluter 2000; Coyne and Orr 2004). This process, termed character displacement (Brown and Wilson 1956), generates shifts in phenotypes associated with resource use (ecological character displacement; Slatkin 1980; Losos 2000; Schluter 2000) or mating behavior (reproductive character displacement; Crozier 1974; Howard 1993; Coyne and Orr 2004). Because character displacement is thought to be a general and important mechanism for promoting adaptive diversification (Schluter 2000; Coyne and Orr 2004), identifying the conditions that foster character displacement is important for understanding the causes of diversity.

Generally, character displacement occurs when selection confers an overall advantage to those individuals with phenotypes most dissimilar from sympatric heterospecifics, and this process can proceed in one of two ways. First, character displacement may shift a population to a new adaptive peak that has fitness equal to or greater than that of the ancestral phenotype (Schluter 2000). Such an outcome may be especially likely to occur in habitats with few competitors and a wide variety of resources to exploit (Simpson 1944, 1953; Schluter 2000). In this case, character displacement may trigger an adaptive radiation, where a single or small group of ancestral species rapidly diversifies into a large number of descendent species that occupy a wide variety of ecological niches (Schluter 2000).

Second, character displacement may generate new phenotypes in sympatry with substantially lower fitness than the ancestral phenotype in allopatry. Such an outcome occurs when sympatric individuals who exhibit the displaced phenotype face a fitness trade-off: they benefit from reduced competition or interference for mates, but suffer costs in other fitness components. Overall, individuals in sympatry with the displaced phenotype will have higher fitness than those without the displaced trait because they experience reduced competition, but they may have reduced fitness relative to individuals in allopatry. In this scenario, character displacement represents a “best of a bad situation” (Maynard Smith 1982) in that it lessens competition but at a cost: the postdisplacement phenotype may have substantially lower fitness than the ancestral predisplacement phenotype. Such a situation places a potential constraint on the evolution of character displacement. If the above costs of character displacement are sufficiently severe, character displacement may not evolve and extinction may occur. Thus, understanding the fitness effects of character displacement is critical to evaluating the conditions under which the process will proceed.

Whether and how character displacement affects fitness of displaced populations relative to ancestral populations remains largely unknown. Indeed, the above alternative fitness effects of character displacement have not been explicitly considered in theoretical (Slatkin 1980; Taper and Case 1992; Schluter 2000; but see Webb 2003) or empirical studies of character displacement (Schluter 2000; Pritchard and Schluter 2001). Consequently, we do not know whether and how character displacement generates fitness trade-offs.

One way that character displacement may produce fitness



FIG. 1. *Spea multiplicata* omnivores (left) and carnivores (right) from the same allopatric pond and of the same age, showing differences in body size between the alternative tadpole phenotypes.

trade-offs in sympatry is when shifts in phenotypes associated with resource use or mate attraction produce correlated changes on other aspects of the phenotype (i.e., through pleiotropy). Pleiotropic effects could have negative impacts on fitness that generate a trade-off between the fitness benefits of avoiding competition on the one hand and the fitness costs of adopting the displaced phenotype on the other hand. Because of the potential for pleiotropic effects to generate fitness trade-offs, pleiotropy could potentially constrain the evolution of character displacement. Yet, the degree to which character displacement affects other aspects of the phenotype beyond the direct targets of selection has rarely been investigated.

Spadefoot toads (genus *Spea*) are ideal for examining these issues. As we discuss in detail below, *S. multiplicata* exhibit both reproductive and ecological character displacement in response to their congener, *S. bombifrons*. In this study, we sought to determine whether reproductive and ecological character displacement has had pleiotropic effects on the evolution of body size in sympatric versus allopatric *S. multiplicata*. Moreover, we investigated whether any such shifts in body size affected the fitness of sympatric individuals relative to allopatric individuals. We show that character displacement to minimize heterospecific interactions can affect phenotypes (e.g., body size) beyond the direct targets of selection. Moreover, we find that, in sympatry, fitness may result from a trade-off between the benefits of avoiding competition and the costs of adopting an alternative phenotype that is less fit than the ancestral type.

Study System

Mexico spadefoot toads (*S. multiplicata*) and Plains spadefoot toads (*S. bombifrons*) coexist in the arid southwestern United States, where they undergo both reproductive and ecological character displacement. As we describe below, the two species differ markedly in mating behavior (Pfennig

2000) and larval development (Pfennig and Murphy 2000, 2002, 2003) where they live together (sympatry), but are similar in these traits where they live separately (allopatry). In addition, their natural history renders them ideal for studying how character displacement affects fitness. Adults emerge from underground for only a few weeks each summer to breed and feed at temporary rain-filled ponds, where their tadpoles are often the only vertebrate species present (Bragg 1965).

Prior work has documented reproductive character displacement in female mate preferences (Pfennig 2000) and male calling behavior (Pierce 1976). In allopatry, *S. multiplicata* females prefer males with fast call rates and choose males that are in better condition (Pfennig 2000). By contrast, in sympatry, *S. multiplicata* females prefer males with slower call rates, presumably because such calls are most dissimilar from *S. bombifrons* males, which call faster than *S. multiplicata* males (Pfennig 2000). Possibly because of this shift in mate preferences, the two species have similar mating calls in allopatry, but are noticeably different in sympatry (Pierce 1976; Pfennig 2000). Also, possibly because of this shift in mate preferences, *S. multiplicata* females in sympatry, unlike those in allopatry, do not choose males that are in good condition (Pfennig 2000).

The two species also have undergone ecological character displacement in expression of larval feeding morphology. Both species potentially 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; Fig. 1; Bragg 1965; Pfennig 1990). Shrimp ingestion potentially triggers development of carnivores from omnivores (Pfennig 1990), but different populations exhibit heritable variation in propensity to express the carnivore morphology (Pfennig and Murphy 2000, 2002).

In allopatry, the two species produce similar proportions of both morphs (Pfennig and Murphy 2003). By contrast, in sympatry, selection to lessen resource competition has caused the two species to diverge in larval development (Pfennig and Murphy 2000, 2002, 2003). Sympatric *S. bombifrons* (the superior competitor for shrimp; Pfennig and Murphy 2000) produce mostly carnivores, whereas sympatric *S. multiplicata* (the superior competitor for detritus; Pfennig and Murphy 2000) produce mostly omnivores (Pfennig and Murphy 2003). Previous experiments indicate that this difference in morph production between species stems from selection to minimize interspecific competition for food (Pfennig and Murphy 2000, 2002). Thus, resource competition has promoted 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).

Earlier work on reproductive and ecological character displacement in *S. multiplicata* suggested that, in addition to changes in mating behavior and feeding morphology, overall body size may undergo a shift between sympatric and allopatric populations. For example, directional selection on male condition in allopatry (but not sympatry) could result in a correlated increase in overall adult body size in allopatry but not sympatry (better condition may fuel enhanced growth). Similarly, because *S. multiplicata* have evolved a reduced propensity to produce the larger carnivore morph (Fig. 1) in sympatry, *S. multiplicata* tadpoles, and, consequently, *S. multiplicata* adults, may be smaller in sympatry than in allopatry.

Our study was designed to address the following two questions. First, are *S. multiplicata* smaller in sympatry than in allopatry with *S. bombifrons*, and, if so, has such a shift in body size likely arisen as a by-product of either ecological or reproductive character displacement? Second, is body size associated with fitness in *S. multiplicata*, and, if so, has character displacement led to reduced fitness in sympatric populations relative to allopatric populations?

MATERIALS AND METHODS

The overall goal of this study was to test whether character displacement has led to the evolution of reduced body size and, hence, diminished fitness in *S. multiplicata*. We addressed this goal by conducting three separate studies.

First, we asked whether *S. multiplicata* are smaller in sympatry than in allopatry. We addressed this issue by sampling numerous adults and tadpoles in natural ponds over 10 years.

Second, because our first prediction was verified (see Results), we evaluated three, nonmutually exclusive hypotheses to explain why *S. multiplicata* adults are smaller in sympatry than in allopatry: (1) selection to minimize inappropriate matings with *S. bombifrons* may have led to the evolution of smaller size as a by-product of reproductive character displacement, (2) selection to minimize resource competition with *S. bombifrons* tadpoles may have led to the evolution of smaller size as a by-product of ecological character displacement, and (3) larger body size may be favored at higher elevations (allopatric sites are generally higher than sympatric sites [see Collection Sites below]; in frogs, larger body

size may be selectively favored at higher elevations [Berven 1982]). We tested whether body size evolution resulted from character displacement (hypotheses 1, 2 above) as opposed to elevational differences (hypothesis 3 above) by determining whether the mean body size of *S. multiplicata* within a population is more highly correlated with the frequency of *S. bombifrons* in that population (a measure of the intensity of competition) than it is with elevation. To determine whether reproductive character displacement may have been in operation, we also examined whether male body size was shifted more than female body size (on the assumption that males would be impacted more than females).

Finally, we asked if character displacement has likely led to diminished fitness in *S. multiplicata*. We addressed this issue by examining whether females in sympatry suffer from reduced fecundity because of their smaller size. We also examined the impact of body size on juvenile survival by rearing tadpoles from both sympatry and allopatry under common conditions.

Collection Sites

During summers 1995–2004, we collected tadpoles and adults of *S. multiplicata* and *S. bombifrons* along a 180-km transect through southeastern Arizona and southwestern New Mexico (Fig. 2). In this region, both species potentially coexist below 1350 m elevation; above 1350 m only *S. multiplicata* is found (Pfennig and Murphy 2000, 2002). We collected adults and tadpoles from low elevation (1200–1350 m) sympatric sites and from nearby (<20 km) higher elevation (1350–1600 m), allopatric sites (i.e., sites containing only *S. multiplicata*). We also sampled adults from a high-elevation and a low-elevation site on the western end of the transect where only *S. multiplicata* occurs. *Spea multiplicata* appears to have competitively excluded *S. bombifrons* from high-elevation ponds: shrimp are scarce in such ponds, and detritus may not have been available to *S. bombifrons* because *S. multiplicata* is better at exploiting this resource (Pfennig and Murphy 2000). Otherwise, allopatric and sympatric sites are similar ecologically (Pfennig and Murphy 2000, 2002) and are potentially within 3 km of each other (Fig. 2).

Adult Body Size, Sexual Dimorphism, and Clutch Size Measurements

We obtained snout-vent length (SVL) measures from 155 adult *S. bombifrons* and 697 adult *S. multiplicata* that were collected at or near eight breeding aggregations in seven different ponds in allopatry ($n = 181$ *S. multiplicata*), and in 17 breeding aggregations in eight different ponds in sympatry ($n = 516$ *S. multiplicata* and 155 *S. bombifrons*; at three of the aggregations, only *S. bombifrons* were collected.). Because they were sampled without replacement, adults gathered from the same pond during different breeding events (both within and between years) were treated separately for the analyses. All adults were sexually mature (as indicated by the presence of nuptial pads in males and eggs in females), and they were measured within one week of capture using hand-held digital calipers. For each of 10 populations, we estimated sexual size dimorphism as $\log(\text{mean male SVL}) - \log(\text{mean female SVL})$ (Arak 1988) using the mean male and

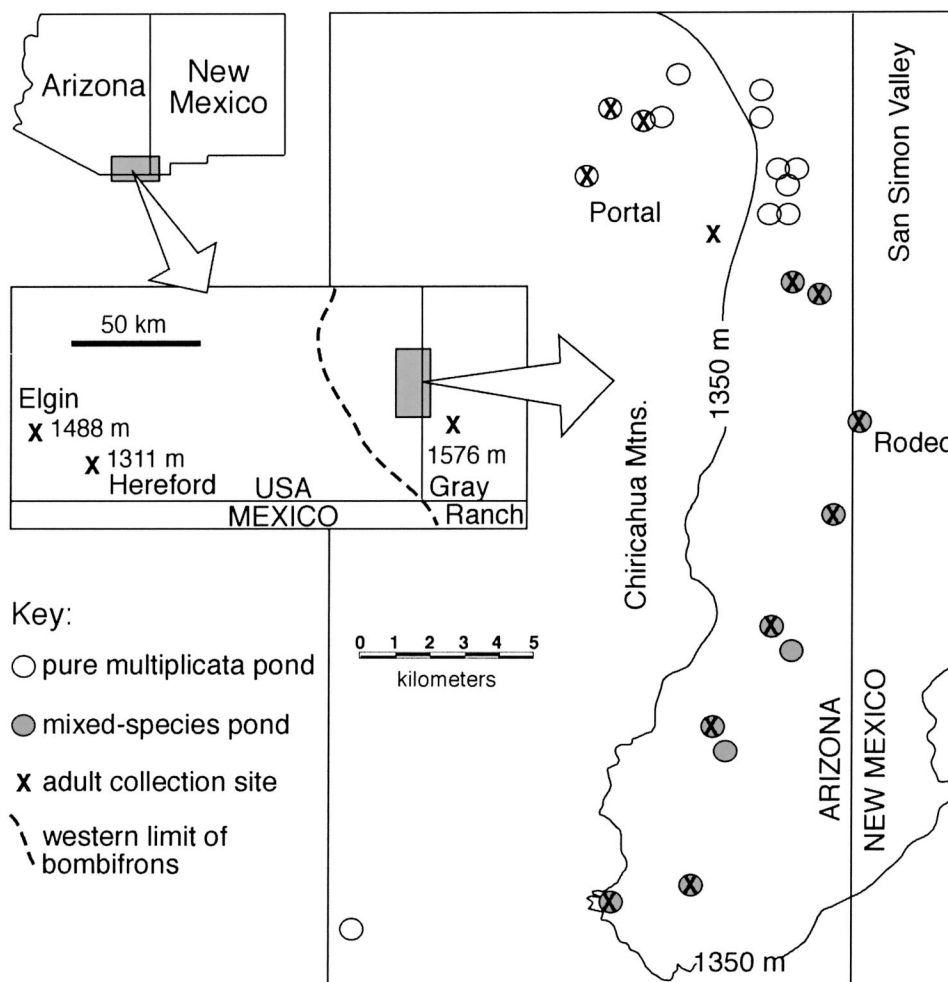


FIG. 2. Map of study area. Circles show locations of breeding aggregations or ponds where tadpoles were collected. X indicates general locations where adults were collected (adults were collected at or near breeding aggregations). At some locations different breeding aggregations occurred in multiple years. They were sampled without replacement and treated as independent.

female SVL calculated for each population separately (these data were not gathered for the remaining populations because adult sex was not recorded with the SVL measure).

To obtain clutch size data, males and females were collected in amplexus from ponds in both sympatry and allopatry. Males and females from the same breeding aggregation were placed together in 13.5 L laboratory aquaria within a few hours of collection and allowed to breed. After oviposition was complete, eggs were counted immediately (for detailed methods, see Pfennig 2000).

Tadpole Identification and Measurements

We sampled at least 20 late-stage (18-day-old) tadpoles from randomly selected sites throughout 18 different natural ponds using a hand-held dip net (most ponds were sampled in at least two different years). Because *Spea* breed in only one night following each pond filling (Bragg 1965; Pfennig 2000), all *Spea* tadpoles from the same pond were of the same age. Within a few hours of collection, we killed the tadpoles by immersion in a 0.1% aqueous solution of tricaine methanesulfonate (MS 222) and preserved them in 95% eth-

anol. Before preserving each tadpole, we took a tissue sample and froze it at -80°C . Later, each tadpole's SVL was measured using hand-held digital calipers. In 1999 we used species-specific allozymes (Simovich and Sassaman 1986), and in 2000–2004 we sequenced a 663-bp region of the mtDNA genome to classify each tadpole as *S. bombifrons* or *S. multiplicata*. We used these genetic data to calculate the frequency of *S. bombifrons* in each population (number of *S. bombifrons* tadpoles/total number of *S. bombifrons* and *S. multiplicata* tadpoles).

Experimental Comparison of Tadpole Survival in Sympatry and Allopatry

We bred three pairs of *S. multiplicata* from allopatry and seven pairs from sympatry. We then randomly selected an equal number of tadpoles from each sibship, pooled them within each of the two treatment groups (i.e., allopatry and sympatry), and randomly assigned them into laboratory tanks in groups of 10. Each tank measured 40 cm \times 27 cm \times 14.5 cm and was filled with 10 L dechlorinated water. The density of tadpoles in each tank was within the range observed in

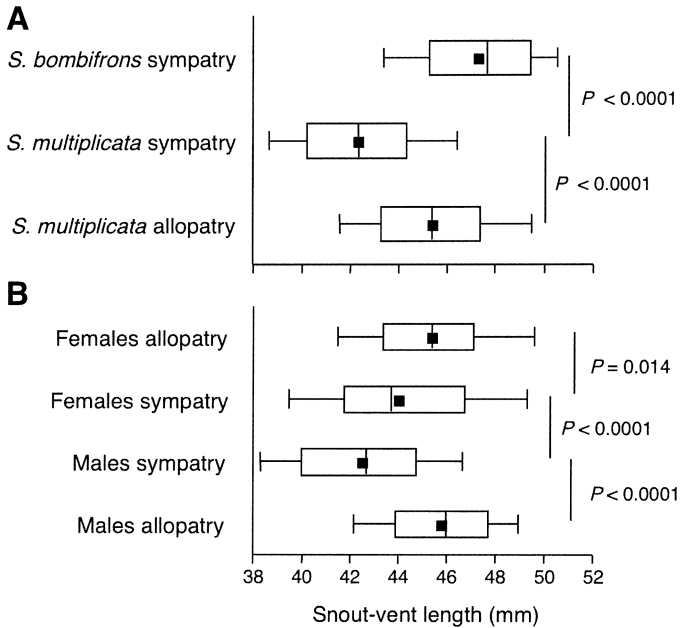


FIG. 3. (A) Snout-vent length (SVL) distributions for *Spea bombifrons* and *S. multiplicata* from populations that do and do not occur with *S. bombifrons* (sympatry and allopatry, respectively). (B) SVL distributions for *S. multiplicata* separated by sex and region. In each panel, black squares show means. Box plots show 10th, 25th, 50th (median), 75th, and 90th percentiles.

the field. We had six replicate tanks for each treatment. Tadpoles in each tank were fed high protein fish food ad libitum and censused daily. For the analysis, we compared the mean percentage in each treatment that survived to metamorphosis.

Statistical Analyses

For comparisons of adult size, we treated each adult as an independent datapoint. This was justified on the basis that most adults from the same breeding pond were likely from different age cohorts and had therefore not likely encountered each other previously (see above). This analysis allowed us to determine whether adults differed in size between sympatry and allopatry. However, for all comparisons of tadpoles and for those relating adult and tadpole size to the frequency of *S. bombifrons* in a population, we pooled all individuals from a single breeding event. These analyses enabled us to determine whether size differences in *S. multiplicata* were related to the presence of *S. bombifrons* per se.

We used *t*-tests to compare population means if the data met parametric assumptions. Where data did not meet these assumptions, we used nonparametric Wilcoxon tests. Because outliers were present in data subjected to correlation analyses, we used nonparametric Spearman rank order correlation analyses that are not sensitive to outliers (Zar 1984).

RESULTS

In sympatry, adult *S. multiplicata* are significantly smaller than *S. bombifrons* (mean difference in adult SVL, *S. bombifrons* – *S. multiplicata* = 4.1 mm, $t_{669} = 13.23$, $P < 0.0001$; Fig. 3A). Moreover, *S. multiplicata* are significantly smaller in sympatry with *S. bombifrons* than in allopatry (mean dif-

ference SVL, *S. multiplicata* from allopatry – *S. multiplicata* from sympatry = 2.3 mm, $t_{695} = 7.64$, $P < 0.0001$; Fig. 3A).

As explained in Materials and Methods, we evaluated whether adult *S. multiplicata* are smaller in sympatry than in allopatry because of: (1) reproductive character displacement, (2) ecological character displacement, or (3) selection favoring larger size at higher elevations.

The shift in body size of *S. multiplicata* is apparently caused by the presence of *S. bombifrons* per se (hypotheses 1, 2 above), and not elevation (hypothesis 3 above). Mean body size of adult *S. multiplicata* in a population is inversely correlated with the frequency of *S. bombifrons* in that population (Spearman rank order correlation coefficient, $r_s = -0.44$, $N = 22$ breeding aggregations, $P = 0.039$). Thus, *S. multiplicata* are smallest when facing the most severe competition from *S. bombifrons*. In contrast, body size does not correlate with elevation across these same populations ($r_s = 0.12$, $N = 22$, $P = 0.573$).

The observed shift in *S. multiplicata* body size in the presence of *S. bombifrons* is attributable at least in part to reproductive character displacement. Because female preferences for good-condition males could indirectly select for increased body size (e.g., good condition may fuel enhanced growth), male body size in *S. multiplicata* may be under selection to increase in allopatry, but not in sympatry where *S. bombifrons* interferes with a female's ability to identify good-condition males (Pfennig 2000). Consistent with this hypothesis, males in sympatry are much smaller than males in allopatry (mean difference allopatry – sympatry: 3.2 mm, $t_{367} = 7.44$, $P < 0.0001$; Fig. 3B). Females in sympatry are also significantly smaller than females from allopatry, but the effect on female size is not as pronounced as for males (mean difference allopatry – sympatry: 1.4 mm, $t_{258} = 2.47$, $P = 0.014$; Fig. 3B). Moreover, the degree of sexual dimorphism is strongly inversely correlated with the frequency of *S. bombifrons* in a population ($r_s = -0.75$, $N = 10$, $P = 0.012$; Fig. 4). When *S. bombifrons* is present, males are significantly smaller than females (mean difference M – F SVL: -1.38 mm, $t_{504} = 4.35$, $P < 0.0001$; Fig. 3B). However, when *S. bombifrons* is absent, males and females are similar in size (mean difference M – F SVL: 0.41 mm, $t_{121} = 0.82$, $P = 0.42$). Anurans typically show reverse sexual dimorphism in size (i.e., males are smaller than females) except when sexual selection favors increased male size (Shine 1979; Andersson 1994). Thus, reproductive character displacement has apparently reduced sexual selection in sympatric populations and thereby indirectly promoted smaller body size.

Ecological character displacement can also explain the observed shift in adult body size. Because *S. multiplicata* have evolved a reduced propensity to produce the larger carnivore morph in sympatry, we hypothesized that *S. multiplicata* tadpoles would be smaller in sympatry than in allopatry (see above). As expected, *S. multiplicata* tadpoles are significantly smaller in sympatry (mean \pm SE SVL = 12.4 ± 1.0 mm, $N = 7$ ponds) than in allopatry (15.5 ± 0.8 mm, $N = 11$ ponds, $t_{16} = 2.46$, $P = 0.026$). Moreover, the mean size of tadpoles in a population is strongly inversely correlated with the frequency of *S. bombifrons* in that population ($r_s = -0.60$, $N = 18$ ponds, $P = 0.009$; Fig. 5). Thus, *S. multiplicata* tadpoles

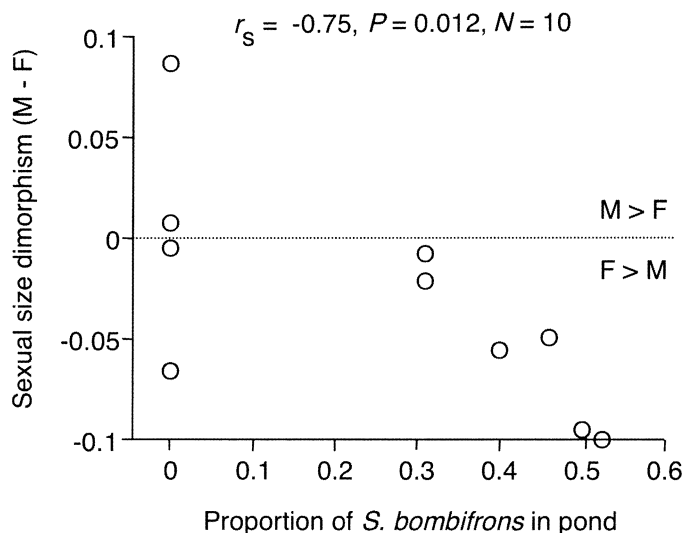


FIG. 4. Relationship between mean sexual size dimorphism of *Spea multiplicata* in each of 10 populations and the frequency of *S. bombifrons* in those populations. At sexual size dimorphism values of zero, males and females are equal in size. Above zero (dotted line), populations show sexual dimorphism, with males larger than females. Below zero (dotted line), populations show reverse sexual dimorphism, with females larger than males.

are smallest when facing the most severe competition from *S. bombifrons* (previous experiments have demonstrated a causal link between the frequency of *S. bombifrons* within a population and size and carnivore frequency among *S. multiplicata* tadpoles; Pfennig and Murphy 2000, 2002). These significant differences between sympatry and allopatry in tadpole size disappeared, however, when we excluded carnivores from the analysis: omnivores were similar in size in sympatry (mean \pm SE SVL 12.3 ± 1.0 mm, $N = 7$ ponds) and allopatry (13.4 ± 0.8 mm, $N = 11$ ponds, $t_{16} = 0.88$, $P = 0.391$). Thus, differences between sympatry and allopatry in overall tadpole size are caused by reduced production of carnivores in sympatry, which in turn reflects ecological character displacement (Pfennig and Murphy 2000, 2002). Because larval size correlates with size at sexual maturity in frogs (Smith 1987), ecological character displacement can partly explain why adult *S. multiplicata* are smaller in sympatry than in allopatry (Fig. 3A).

Smaller body size is associated with lower fitness in many species (Kingsolver and Pfennig 2004), and in sympatric *S. multiplicata*, the shift toward smaller size appears to have lowered mean individual fitness in at least two ways. First, when we compared survival of tadpoles from sympatry versus allopatry under identical conditions, the former had lower survival, possibly because of their smaller size (mean \pm SE % survival in sympatry = $48.3 \pm 7.5\%$, allopatry = $73.3 \pm 7.1\%$, $t_{10} = 2.41$, $P = 0.036$). Second, body size correlates significantly positively with clutch size in our populations: smaller females produce fewer eggs ($r_s = 0.40$, $N = 51$, $P = 0.004$; Fig. 6). Because females are smaller in sympatry, we hypothesized that female clutch size would be smaller in sympatric populations. As predicted, we found that, on average, the clutches of sympatric females were 16.5% smaller than those of allopatric females. The mean \pm SE clutch size

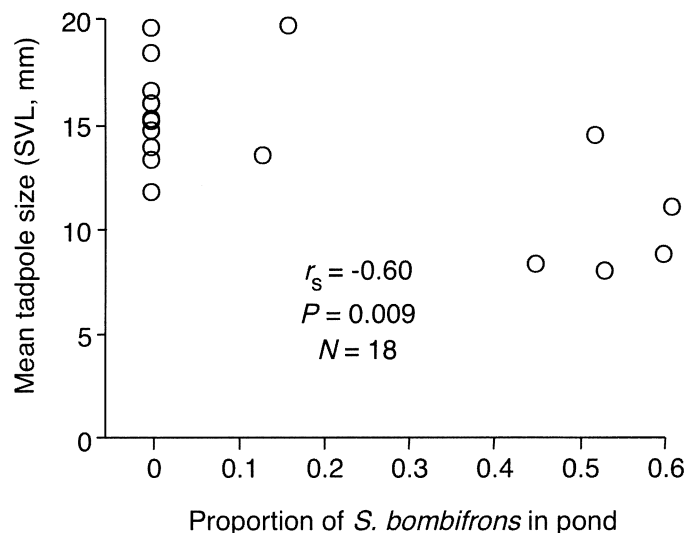


FIG. 5. Relationship between the frequency of *Spea bombifrons* and tadpole size of *S. multiplicata*. Frequency of *S. bombifrons* indicates the strength of competition experienced by *S. multiplicata* tadpoles.

for sympatric females was 966 ± 64 , which was significantly smaller than the mean clutch size in allopatry of 1158 ± 104 (Wilcoxon normal approximation, $Z = 1.90$, $P = 0.029$ [one tail]). Thus, by indirectly promoting the evolution of smaller size, character displacement appears to reduce larval survival and female fecundity in sympatry relative to allopatry.

DISCUSSION

Shifts in adult body size in *S. multiplicata* (Fig. 3A) appear to result from both reproductive and ecological character displacement. Although elevational differences could have potentially explained differences in body size between sympatric and allopatric populations (sensu Berven 1982), we found no support for this hypothesis. Moreover, our results suggest that changes in *S. multiplicata* body size are not mediated by either ecological or reproductive character displacement acting alone. Whereas ecological character displacement generates smaller tadpoles that may become smaller adults in sympatry (Fig. 3A), this process cannot explain the relative changes in male and female body size (Fig. 3B) that are best accounted for by reproductive character displacement. Because anurans typically show reverse sexual dimorphism in the absence of sexual selection on males, our finding that reverse sexual dimorphism disappeared in allopatry indicates that males in these populations are under directional selection to increase in size (and females may experience a correlated response). Thus, reproductive character displacement has apparently reduced sexual selection in sympatric populations (a result consistent with earlier findings in *S. multiplicata*; Pfennig 2000) and thereby indirectly promoted smaller body size.

Although we cannot say with certainty that the presence of *S. bombifrons* has caused the observed shift in *S. multiplicata* adult body size, previous experiments have demonstrated a causal link between the frequency of *S. bombifrons* in a population and *S. multiplicata* tadpole size (Pfennig and

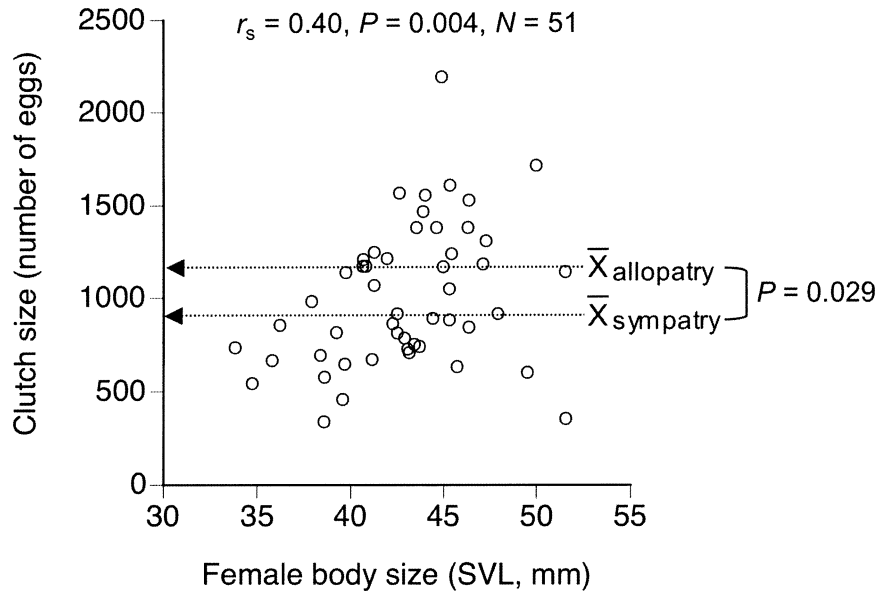


FIG. 6. Relationship between body size and clutch size in *Spea multiplicata* as well as differences in mean clutch size in sympatry and allopatry.

Murphy 2002). Because tadpole size may correlate positively with adult size in anurans (Smith 1987), these experimental results suggest that the presence of *S. bombifrons* may indeed cause a shift toward smaller adult size in *S. multiplicata*. This conclusion is reinforced by our finding that mean body size of adult *S. multiplicata* in a population is inversely correlated with the frequency of *S. bombifrons* in that population (see Results). Thus, *S. multiplicata* are smallest when facing the most severe competition from *S. bombifrons*, which suggests that shifts in adult body size in *S. multiplicata* are likely caused by the presence of *S. bombifrons* per se.

Do differences in adult size between sympatry and allopatry reflect canalized, inherited differences or do they reflect an induced response to the presence of the competitor (i.e., phenotypic plasticity)? Previous experiments have revealed that ecological character displacement is mediated, in part, by canalized differences in propensity to produce alternative tadpole phenotypes (Pfennig and Murphy 2000, 2002). Even when reared under common conditions from fertilization, *S. multiplicata* from sympatry produce mostly the smaller omnivore morph (Fig. 1), whereas those in allopatry produce both morphs, suggesting that differences between regions are canalized. Because tadpole size may dictate adult size, differences in adult size between sympatry and allopatry are also likely canalized. However, additional studies are needed to test this assumption.

The degree to which reproductive and ecological character displacement act jointly to affect the evolution of body size in this system remains unclear. If mating behaviors are correlated with juvenile feeding morphology, reproductive and ecological character displacement may reinforce one another in this system. However, if mating behaviors and juvenile feeding morphology are not related, both processes may have coincidentally resulted in reduced body size in sympatry without directly reinforcing one another. The manner in which reproductive and ecological character displacement in-

teract with one another has rarely been evaluated (but see Albert and Schluter 2004). Because species that compete for resources are also likely to interact during mating, reproductive and ecological character displacement may often be intertwined. Additional data are required to ascertain the degree to which these processes interact to shift phenotypes in response to heterospecifics.

Adult body size is likely not the direct target of selection to reduce resource competition and mating interactions with *S. bombifrons*. Specifically, we hypothesize that directional selection on male condition in allopatry but not sympatry (as mediated by female mate choice; Pfennig 2000) has indirectly increased adult body size in allopatry but not sympatry (better condition may fuel enhanced growth and larger size in allopatry). Similarly, because *S. multiplicata* have evolved a reduced propensity to produce the larger carnivore morph in sympatry (Pfennig and Murphy 2000, 2002, 2003), *S. multiplicata* tadpoles, and, consequently, *S. multiplicata* adults, may be smaller in sympatry than in allopatry. Thus, the shift in adult body size has likely occurred as an incidental by-product of reproductive and ecological character displacement acting to promote divergence between these species in mating behavior and larval development, respectively. Body size therefore is not likely undergoing character displacement per se. Instead, body size evolution is likely a pleiotropic effect of changes brought about by ecological and reproductive character displacement in other aspects of the phenotype. This conclusion that body size evolves as a by-product of character displacement contrasts with results from threespine stickleback fish, for example, which also undergo ecological and reproductive character displacement, but in which body size is under direct selection acting on mating preferences (Albert and Schluter 2004).

The shift in *S. multiplicata* body size has critical ramifications for mean population fitness in sympatric versus allopatric populations. We found that sympatric tadpoles had

significantly lower survival than allopatric tadpoles. This pattern could have resulted from reduced body size of sympatric tadpoles attributable to ecological character displacement in feeding morphology. In conjunction with reduced offspring survival in populations with reduced adult body size, we found that smaller females have smaller clutch sizes than larger females. Indeed, sympatric female clutch size was 16.5% smaller on average than allopatric female clutch size (Fig. 6). That sympatric *S. multiplicata* populations have lower survival and fecundity than allopatric populations suggests that character displacement may shift sympatric populations to a lower adaptive peak than that occupied by populations possessing the ancestral predisplacement phenotype. Thus, character displacement may represent the “best of a bad situation” (Maynard Smith 1982) in that *S. multiplicata* benefit by avoiding competition and mating interactions with *S. bombifrons* but at a cost in terms of offspring survival and reduced female fecundity.

Finding that character displacement may generate fitness trade-offs has important implications for understanding when and how character displacement will occur. First, such fitness trade-offs may explain why traits that evolve in sympatry often do not spread back into allopatry even in the face of high gene flow (for discussion see Servedio and Noor 2003 and references therein). For example, *Drosophila pseudoobscura* exhibits high intraspecific gene flow (see Noor et al. 2000 and references therein), yet females express divergent mating behaviors between sympatric and allopatric populations (Noor 1995; Noor and Ortiz-Barrientos 2005). If traits that evolve in sympatry confer a selective disadvantage in allopatry, then phenotypes that evolve in response to heterospecifics should remain localized in sympatry. Character displacement’s hallmark pattern of divergent traits in sympatry and allopatry suggests that the fitness trade-offs in sympatric populations that we have observed here may be a common feature of character displacement.

Another implication of fitness trade-offs stemming from character displacement is increased extinction risk for sympatric populations relative to allopatric populations. The predominant view of competitive interactions between species is that one of two alternatives will attain (Losos 2000): (1) character displacement will enable stable coexistence of the competing species; or (2) competitive exclusion will result when the superior competitor drives the inferior one to extinction. Yet, fitness trade-offs may place sympatric populations at risk of extinction despite the evolution of character displacement. For example, lower survival and fecundity in sympatric populations may increase their risk of extinction. Indeed, recent theory has revealed that the evolution of a population by individual-level natural selection can paradoxically reduce mean population fitness, which may ultimately bring about the population’s demise (i.e., a “Darwinian extinction”; Webb 2003). Although these models indicate that competitive interactions may be a leading cause of such extinctions (Doebeli and Dieckmann 2000; Webb 2003), empirical data examining character displacement’s effect on fitness have been lacking (Webb 2003). Our finding that sympatric populations face fitness trade-offs reveals a potentially critical constraint on the evolution of character displacement, and it illustrates how otherwise adaptive evo-

lution can result in decreased mean population fitness in sympatry relative to allopatry, which may ultimately render sympatric populations more susceptible to extinction (Webb 2003).

By causing interacting species to diverge from one another, character displacement may contribute to the diversification of species into new niches (Schluter 2000) and possibly even the origin of new species (Howard 1993; Coyne and Orr 2004). For this reason, character displacement has long been considered a major cause of adaptive diversification (e.g., Darwin 1859; Lack 1947; Brown and Wilson 1956). However, if fitness trade-offs in sympatric populations increase their risk of extinction, character displacement may not always promote diversity as expected. Thus, although character displacement is typically viewed as a key diversifying force in evolution (Darwin 1859; Lack 1947; Brown and Wilson 1956; MacArthur and Levins 1964; Grant 1972; Schluter 2000; Coyne and Orr 2004), natural selection to lessen competition or mating interactions between species may fail to generate diversification depending on the nature of fitness trade-offs that arise in sympatry. Clarifying the conditions that promote these alternative outcomes of heterospecific interactions will shed light on how local diversity originates and is maintained.

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