2009-07-10

Co-occurrence with a congeneric species predicts life history and morphological diversification in the Mexican livebearing fish Poelicopsis baenschi

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Co-occurrence with a congeneric species predicts life history and morphological diversification in the Mexican livebearing fish *Poeciliopsis baenschi*

by

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A thesis submitted to the faculty of Brigham Young University in partial fulfillment of the requirements for the degree of

Master of Science

Department of Biology
Brigham Young University
August 2009

BRIGHAM YOUNG UNIVERSITY

GRADUATE COMMITTEE APPROVAL

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This thesis has been read by each member of the following graduate committee and has been found to be satisfactory for university publication.

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ABSTRACT

Co-occurrence with a congeneric species predicts life history and morphological diversification in the Mexican livebearing fish *Poeciliopsis baenschi*

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Understanding why some species coexist and others do not remains one of the fundamental challenges of ecology. While several lines of evidence suggest that closely related species are unlikely to occupy the same habitat because of competitive exclusion, there are many cases where closely related species do co-occur. Research comparing sympatric and allopatric populations of co-occurring species provides a framework to understand the role of phenotypic diversification in species coexistence. In this study I focus on the livebearing fish *Poeciliopsis baenschi* and ask if differences in phenotypic traits among populations can be explained by the presence or absence of the congeneric species *P. turneri*. I focus on phenotypic divergence in life history traits and in body shape, two sets of integrated traits likely to respond to variation in competition. Additionally, I compare explore the effects of sympatry and allopatry on sexual dimorphism. I take advantage of a natural experiment in western Mexico where *P. baenschi* co-occur with *P. turneri* in some locations (sympatric populations) but also exist in isolation in other locations (allopatric populations). My results show that sympatric populations of *P. baenschi* differed significantly in life history traits and body shape when compared to their allopatric counterparts. Additionally, the amount of sexual

dimorphism differed between sympatric and allopatric populations of *P. baenschi*, suggesting different constraints might exist in sympatry and allopatry for sexual dimorphism. Lastly, I explore my results in the context of trait evolution as it relates to species coexistence.

KEYWORDS: geometric morphometrics – life history theory – Poeciliidae – resource competition – sexual dimorphism – sympatry

ACKNOWLEDGMENTS

I sincerely thank Dr. Jerald B. Johnson for being a mentor and advisor for my thesis. I also thank my committee, Drs Mark C. Belk, Byron J. Adams, and Russell B. Rader for all their help reading the manuscript and providing constructive comments. In addition, I thank Joshua Rasmussen and Eric Billman for providing statistical advice and feedback. UNAM and J. J. Zuñiga-Vega provided permits and logistical support during fieldwork. This study was supported by a grant from BYU Department of Biology, BYU Office of Graduate Studies, and the Roger Sant Endowment to which I am very appreciative of. Also, I thank Eric Schott, Ashley Camargo, and Kent Stilson for all their help in the field and in the laboratory collecting and preparing data. I am very grateful to my parents and family who have given me strong encouragement in my educational pursuit. Lastly, I thank my husband Jacob for all his support and encouragement.

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INTRODUCTION

Ecological theory predicts that closely related species with overlapping niches are unlikely to occupy the same habitat because one species will competitively exclude the other (Gause, 1932; Hutchinson, 1959; Schluter, 2000). There are however, many cases where closely related species do co-occur. A substantial body of theoretical work has been produced to explain how evolutionary divergence between co-occurring species can permit the persistence of taxa with similar niches (Ackerly, Schwilk, & Webb, 2006; Brown & Wilson, 1956; Colwell & Futuyma, 1971; Pianka, 1974). One prediction derived from this work is that sympatric and allopatric populations should show significant divergence in phenotypic traits (Pianka, 1988).

Several studies across a range of taxa support the expectation that conspecific populations will show phenotypic divergence in sympatry compared to allopatry. These include divergence of jaw morphology in salamanders (Adams & Rohlf, 2000), mouth positioning in stickleback fish (Schluter & McPhail, 1992), beak size in ground finches (Boag & Grant, 1984), life history strategies in desert shrubs (Verhulst et. al, 2008), and male mating calls in ground crickets (Benedix & Howard, 1991). Recent studies of adaptive divergence have focused on dissecting single traits into their component parts (e.g., song pulse, pulse rate, and song duration are all parts of the song call; Lemmon, 2009) yielding additional insight into fine-scale trait divergence among closely related species. However, relatively few studies have compared phenotypic divergence for different suites of traits in response to the presence of conspecific populations. Such studies could be particularly valuable to help identify aspects of the niche that are important in permitting or limiting species co-occurrence (Hutchinson, 1959; Chase & Leibold, 2003). Of additional interest is if males and females respond similarly to the presence or absence of potential competitors. Males and females often show differences in behavior, morphology, and reproduction (Hendry et al., 2006) and such differences may result in different responses to the presence of a congeneric species. What is needed to address these questions is a natural system of two closely-related species where populations occur in both sympatry and allopatry and where

multiple phenotypic traits can be compared across both populations and between males and females.

Freshwater fishes of western Mexico provide an excellent model to examine divergence of different traits under sympatric versus allopatric conditions. In this study I focus on the livebearing fish *Poeciliopsis baenschi*. This species is found in several drainages along the central-western coast of Mexico: in some locations it co-occurs with a closely related species, *P. turneri*; in other locations it is the only livebearing fish species present (Figure 1; Miller, 2005). This contrast provides a natural experiment where phenotypes of isolated *P. baenschi* populations (allopatric treatment) can be compared to phenotypes of *P. baenschi* that co-occur with *P. turneri* (sympatric treatment).

While many different types of traits can diverge between sympatric and allopatric environment, the primary goal in this study was to determine if the presence of the congener *P. turneri* predicted differences in life history and body shape in *P. baenschi*. I focused on these traits because in poeciliids they show a phenotypic response to competition (Bashey, 2008; Bisazza & Pilastro, 1997) and show differences between males and females (Farr, 1989). The second goal of this study was to compare observed divergence between males and females to better understand if divergent selection affects the sexes similarly in life history strategies and affects sexual dimorphism in body shape. Predictions from life history theory and empirical work on shape evolution provide a framework to understand phenotypic diversfication in *P. baenschi*. For example, if co-occurrence with *P. turneri* results in reduced resource availability, life history theory predicts that at sympatric sites, *P. baenschi* should mature at a larger size, invest less in reproduction, and have larger but fewer offspring (Bashey, 2008; Roff, 2001). Empirical work on fish body shape evolution suggests that competition for resources could alter morphology in a variety of ways, including changes in jaw morphology to better accommodate certain prey (Reuhl & DeWitt, 2005; Schluter & McPhail, 1992), or could have an indirect effect on morphology due to different growth rates (Arendt & Reznick, 2005). Competition might also affect the amount of sexual size dimorphism between males and females; empirical work across several species shows

that under allopatric conditions, sexual dimorphism is more pronounced than when a population occurs with a closely related (Simberloff et al., 2000). Hence, my focus was first to ask if differences in life history and body shape among population of *P. baenschi* could be predicted by the presence or absence of the congener *P. turneri*. My second objective was to compare the degree of body shape divergence in sympatry and allopatry between sexes.

MATERIAL AND METHODS

STUDY SYSTEM

Poeciliopsis baenschi is a livebearing fish in the family poeciliidae. Like all other species in the family, *P. baenschi* males internally inseminate females using a modified anal fin (gonopodium) to transfer sperm and females give live birth to free swimming offspring. Females are capable of simultaneously carrying multiple broods at different stages of embryonic development, a phenomenon known as superfetation. Individuals reproduce year-round and reproductively mature females show marked abdominal distention as a result of pregnancy.

Poeciliopsis baenschi has a relatively small distribution in western Mexico (Figure 1). Within its range, this species occurs in two distinct assemblage types—co-occurring with the closely related *P. turneri*, and in other locations occurring alone. Work by Mateos et al. (2002) on the phylogeny and phylogeography of *Poeciliopsis* in western Mexico indicates that *P. baenschi* and *P. turneri* are not sister species, but rather are members of two distinct monophyletic clades. Hence, it appears that the two species have come into secondary contact in the Rio Purificación drainage where both species now occur. This natural experiment allows me to compare phenotypes of populations of *P. baenschi* that co-occur with *P. turneri* to those that occur in isolation outside of the distribution of *P. turneri*.

I collected *P. baenschi* from 15 localities throughout its distribution in western Mexico (Figure 1). All collections were made during the dry season (between the months of May and June). My sampling resulted in six localities where *P. baenschi* and *P. turneri* co-occur and nine localities where *P. baenschi* occurs without *P. turneri* present. Fish were collected with a hand-held seine net (1.3 m x 5 m; 8 mm mesh size). Approximately 200 individuals were taken from each site to ensure adequate representation of both mature and immature females for use in the life history analysis

(see below). All fish were preserved in the field in ethanol and transported to the laboratory for further data collection.

Studies such as this, which rely on comparisons from field-caught samples, are potentially subject to the effects of extraneous environmental factors. Hence, I chose collection sites that were as similar to each other as possible with respect to potentially confounding ecological factors. To evaluate homogeneity environmental conditions, I collected and compared data on stream velocity, pH, and water temperature from each site; these are factors known to affect life history phenotypes and body shape in other poeciliid systems. However, I found no statistical difference for any of these factors between sympatric and allopatric sites (stream flow: $t = -0.66$, $p = 0.59$; temperature: $t = 2.06$, $p = 0.06$; pH: $t = 0.58$, $p = 0.53$) (Table 1).

QUANTIFYING PHENOTYPIC TRAITS

Life History Phenotypes

I measured six life-history traits for each population: (1) male size at maturity; (2) female size at maturity; (3) number of broods per female, a measure of superfetation; (4) reproductive allotment per brood; (5) number of offspring per brood; and (6) offspring size. All life-history data were collected in the laboratory from the alcohol-preserved specimens using methods described by Johnson & Belk (2001) and Zúniga-Vega, Reznick, & Johnson (2007). In brief, because males cease to grow upon maturation (unpubl. data) male size at maturity was estimated as the mean standard length (SL; tip of the mouth to the end of the vertebral column) of adult males in each population. Males were scored as mature if they showed complete development of the gonopodium. Females continue to grow after maturation. Hence, female size at maturity was determined by dividing females into 2-mm size classes and identifying the minimum size class at which at least half of the females contained developing offspring (stage 3 or greater following Haynes, 1995). Numbers of broods per female were counted directly via dissection; distinct broods were identified using the 11-stage classification system

outlined in Haynes (1995). Reproductive allotment per brood was measured by weighing the mass of the brood with the most advanced developmental stage in each female. Number of offspring per brood equaled the total number of individuals in each developing brood. Offspring size equaled the average per capita dry weight of developing offspring. Only females with developing embryos were included in the estimates of reproductive allotment, number of offspring and offspring size. Dry masses were measured for both embryos and adult females (digestive tract removed) after 24 h in a desiccating oven heated to 55^{o} C.

Body Shape

To assess body shape variation I used landmark-based geometric morphometrics (Adams, West, & Collyer, 2007). I photographed the left lateral side of all reproductively mature fish. Using these images, I digitally marked the location of 11 anatomical landmarks using the shape analysis program TPSDIG (Rohlf, 2004). From these two-dimensional landmarks, I computed a set of 'shape variables' for each fish using the thin-plate spline approach (Zelditch et al. 2004) in program TPSRELW (Rohlf, 2002). This resulted in a set of relative warp (RW) scores for each individual, which were used as inputs for the statistical analyses.

STATISTICAL ANALYSES

Life history traits

One of my goals was to test for differences in life history traits between sympatric and allopatric populations of *P. baenschi*. To compare superfetation between habitat types, I treated the number of broods as a categorical response variable, where females were identified as either carrying one brood or greater than one brood. This was justified because although the maximum number of broods observed was three, females carrying three broods were rare (4.3%) with the majority of females carrying either one or two broods. Given the characterization of superfetation as a binomial trait, I used logistic regression to test for a difference between sympatric versus allopatric populations. I

included 'habitat type' as a main effect in this model, 'female dry mass' as a covariate, and an interaction term between these two factors. 'Population' was also included as a random variable in the model. I tested for differences among all other life history traits using a general linear model (GLM) framework (Littell et al., 1996). Male size at maturity and female size at maturity were both evaluated using an analysis of variance (ANOVA). Reproductive allotment per brood, number of offspring per brood, and offspring size were each evaluated by analysis of covariance. Each of these models included habitat type (sympatric versus allopatric) as the fixed main effect and population locality as a random effect, making these mixed models. Some of the models also included covariates. Maternal body size (mass) can covary with reproductive allotment, number of offspring, and size of offspring. Hence, it was included as a covariate in each of these models. Additional covariates were included for number of offspring per brood (number of broods per female) and for individual embryo size (brood developmental stage). To meet the assumptions of these statistical tests, the following transformations were made: female dry mass, reproductive investment per brood, and individual embryo size were $\log_{10}$ transformed; and number of offspring per brood was square root transformed. I also included the interaction between habitat type and female mass to compare how traits change in sympatry and allopatry as a function of female body size.

Body shape

I compared relative warp (RW) scores across populations and between males and female using a mixed-model multivariate analysis of variance (MANOVA) to evaluate the effect of 'habitat' (allopatric or sympatric) and 'sex' on body shape while adjusting for the random effects of 'population' and 'individuals' among populations. Individual RW scores were used as dependent variables and I obtained least square means values for each RW. To accommodate multiple response variables (RW scores) in a mixed-model design, I treated response variables as a repeated measure on a given individual. Habitat type and sex, along with their interaction, were used as explanatory variables. Relative warps were generated from a principal components analysis and represent

orthogonal axes of shape variation that account for decreasing amounts of total variation. Because of this inherent ordering, it is the interaction between other main effects and the "order" variable that tells if a given fixed effect has a significant effect on at least one of the shape variables (Zelditch et al, 2004). Hence, I included an additional 'order' term that encompasses the order of RW scores as an explanatory variable along with its two- and three-way interactions with sex and habitat.

The two- and three-way interaction terms, and the order term, were all significant (see Results below) indicating the phenotypic change between the two habitats also differs between sexes. Consequently, to better understand biologically how the interaction terms differed, I used a trajectory analysis (Collyer & Adams, 2007) to compare the degree of divergence between allopatric and sympatric populations for males and females. I calculated phenotypic change vectors from least square means to describe the magnitude (length) and direction (angle) of change. Additional factors (not related to being in sympatry) may result in a significant interaction; hence, I also used a permutation procedure to test if the observed differences in phenotypic change trajectories are greater than expected from random pairs of trajectories as described (following Adams et al. 2007). The permutation procedure used residuals from the reduced model (no sex by habitat interaction) with these residuals then randomly assigned to individuals for each permutation used to generate the random distribution. Attributes of the random trajectories were calculated from the least square means from the full model using the randomized values. This was repeated 999 times and attributes of the random trajectories were compared those of the observed allopatric and sympatric trajectories.

RESULTS

Life History

Poeciliopsis baenschi populations that co-occur with the congener *P. turneri* had different life-history phenotypes than their counterparts from populations where *P. turneri* is absent. However, not all life history traits showed the same level of divergence (Table 3). There was no difference in size at maturity among males between habitat types (Figure 2A: sympatry = 19.5 ± 0.5; allopatry = 19.6 ± 0.5). However, females showed pronounced differences in size at maturity between habitat types (Figure 2B: sympatry = 21.0 mm ± 0.5; allopatry = 18.6 mm ± 0.5). Interestingly, females from allopatric sites were smaller on average at first reproduction than males from these sites. Also, four of the six allopatric populations matured at the 18mm size class while no sympatric populations matured below 20 mm (Table 2). There was also no difference in the degree of superfetation between habitat types (sympatric = 1.56 broods ± 0.04, allopatric = 1.58 broods ± 0.04) (Figure 2C). However, female size was a significant predictor of superfetation: larger females had more broods. Sympatric populations allocated less energy to reproduction per brood than allopatric populations (sympatric: 2.7 mg ± 0.4; allopatric: 4.4 mg ± 0.6) (Figure 2D). The covariate female mass and the covariate by habitat interaction were also significant (Table 3), with larger females showing higher reproductive allotments than smaller females. Individuals from sympatric populations of *P. baenschi* had significantly fewer offspring per brood than females from allopatric populations (Figure 2E: sympatry: 2.7 offspring ± 0.8, allopatric: 5.3 offspring ± 1.1). Moreover, the covariate female mass, and the interaction between female mass and habitat were both significant (Table 3). Overall, larger females had more offspring per brood than smaller females, but large sympatric females had significantly fewer offspring than large allopatric females. The average size of individual offspring did not differ significantly between habitat types (Figure 2F; sympatric: 1.1 mg ± 0.2; allopatric: 0.9 mg ± 0.2). The covariate females mass was not significant, but the covariate by habitat interaction was for offspring size. Small sympatric females had larger offspring

than small allopatric females; however, as females became larger, both sympatric and allopatric populations had similar sized offspring.

Body Shape

Poeciliopsis baenschi populations that co-occur with the congener *P. turneri* had a different body shape than their counterparts from populations where *P. turneri* is absent (Table 4). For both males and females, sympatric populations had a more robust body shape (Figure 3). In addition, sympatric and allopatric populations showed differing amounts of body shape divergence. Phenotypic change vectors revealed that allopatric populations showed greater divergence than sympatric populations ($\Delta D=0.007$ $p < 0.01$). However, the angle between these vectors was not significantly different ($\theta = 2.89^{o}$; $p = 1.0$) (Figure 3) indicating males and females do not differ in the direction of divergence, but in the amount of divergence. The first three relative warps explain 92.7% of shape variation.

DISCUSSION

The ability for closely related species to co-exist may depend on a shift in traits of one or both species to permit the joint use of resources (Schluter, 2000). While many empirical studies of species co-existence commonly identify a primary trait that diverges to permit species co-existence (reviewed in Robinson & Wilson, 1994), studying the divergence of multiple traits and comparing males and females may provide additional insight into how organisms respond to the presence of competitors. Additionally how sexual dimorphism is affected by the presence of a congener may provide further understanding for how males and females partition niches within species. In this study, I show that sympatric populations of *P. baenschi* differ significantly from their allopatric counterparts for both life history traits and body shape. Interestingly, males and females show different responses in life history. Sympatric females mature at a larger size, have lower reproductive investment, and produce fewer offspring than their allopatric counterparts; males show no significant differences in life history between sympatric and allopatric populations. The relative contribution of genetic divergence and phenotypic plasticity of this sex-specific response to the presence of a congener remains unknown. However, the body shape analysis reveals that sex explains most variation in body shape (Figure 3). While sympatric populations are significantly different than allopatric populations, the primary axis of body shape variation is due to differences between the sexes. Here I explore patterns of phenotypic divergence between sympatric and allopatric populations of *P. baenschi* relative to theoretical predictions and explore the implications of these findings for understanding species co-existence patterns.

LIFE HISTORY DIVERGENCE

Why should the presence of *P. turneri* result in life history shifts in *P. baenschi*, and why do females show divergence but not males? One possibility to explain life history shifts in females is that the presence of the closely related species results in increased competition for limited resources. Poeciliid growth rates and maturation patterns are strongly influenced by food availability (Bashey, 2008; Snelson, 1989). If per capita

resource availability is lower in sympatric sites, what kinds of life history shifts might we expect? Chronically low resource environments favor the evolution of slow growth rates, resulting in a larger size at maturity and less energy allocated to reproduction (Arendt & Reznick, 2005; Roff, 2001). Consistent with these empirical findings in other systems, I find that *P. baenschi* females from populations that co-occur with *P. turneri* mature at larger body sizes and have lower reproductive investment than their allopatric counterparts. Additionally, sympatric females had fewer offspring than allopatric females. In controlled laboratory studies of a related fish, *Poecilia latipinna*, low-resource environments result in fewer offspring (Trexler, 1997). However, one prediction seen in many organisms that was not observed in this system is a life history tradeoff between number of offspring and offspring size (Messina & Fox, 2001). The theoretical prediction for this tradeoff is that having fewer offspring should also favor having larger size offspring because larger offspring are better competitors (Bashey, 2008). In this system, females in sympatry have fewer offspring than females in allopatry, but offspring size does not differ. Morphological design may explain this finding (Congdon & Gibbons, 1987). In many fishes intestinal length varies with diet. In poeciliids, herbivorous fish have longer intestines than omnivorous fish, and both have longer intestines than carnivorous fish (Kramer & Bryant, 1995). An increase in intestinal length size in the abdominal cavity may hinder the capacity for females to carry additional offspring. Although this study focused on identifying differences between sympatry and allopatry, these results suggest various factors may contribute to the life history strategies that deserve further investigation.

Superfetation is a reproductive strategy thought to have evolved in females as a consequence of constraints in body design (Thibault & Schultz, 1978, Reznick & Miles, 1989). A recent finding in the livebearing fish *Poeciliopsis turrubarensis* is that more fusiform body shapes in females are strongly correlated with higher levels of superfetation (Zuniga-Vega et al, 2007). The explanation for this finding is that more fusiform body shape is advantageous in streams with high flow rates to enhance swimming performance in fishes and hence, superfetation compensates reproductively for the morphological constraint of a fusiform body shape. In this system, the number

of broods does not differ significantly between environments. This may be explained by the fact that no observable differences in abdominal or caudal region of the females indicate abdominal morphology is being constrained in one environment or the other. Further, stream velocity does not differ significantly between allopatric and sympatric sites. Thus in keeping with the morphological constraint hypothesis, the level of superfetation would not be expected to diverge in this system as observed.

Although females show considerable differences in life history traits between habitat types, males do not. Differences in size at maturity for females, but not males, suggests that the presence of *P. turneri* may affect *P. baenschi* females differently than *P. baenschi* males. One possible explanation for this pattern can be found in other species where male and female individuals are spatially segregated, prefer different microhabitats, and use different food resources (reviewed in Hendry et al, 2006). It is unclear if differences in resource use exist between sexes in *P. baenschi*, but these findings with respect to size at maturity point to this as a fruitful direction for future work.

BODY SHAPE VARIATION

There are significant differences in body shape between sympatric and allopatric populations of *P. baenschi*. However, the most profound difference in body shape is between males and females, regardless of habitat type. These differences are depicted along RW1, which distinguishes males from females and hence captures the amount of sexual dimorphism exhibited between the sexes. Sexual dimorphism may evolve for a variety of reasons including different social behaviors or habitat preferences (reviewed in Mazer & Damuth, 2001). In *P. baenschi* as well as many poeciliids, mature females are larger than mature males (Miller, 2005) and the size dimorphism may be due to difference in reproductive efforts and reproductive behaviors between the sexes such as male-male competition (Bisazza & Pilastro, 1997; Parker, 1992). Of particular interest in this study is the finding that a greater amount of sexual dimorphism is seen in allopatric populations.

Theoretical models suggest that in allopatric environments, taxa are likely to show greater levels of phenotypic divergence compared to sympatric environments (Schluter, 1996; Selander, 1966), a phenomenon called 'character release' (Robinson & Wilson, 1994). The rationale is that a lack of competition allows for taxa to exploit more novel niches or resources and hence, evolve greater amounts of phenotypic variation. Several empirical studies support this theoretical model of greater diversity for phenotypic traits in environments with fewer taxa such as beak size in finches (Schluter, 1996) and male body size in anolis lizards (Schoener, 1969). In guppies, males and females show different responses in body shape to the same environmental factors (Hendry et al. 2006). Sexual dimorphism may likewise show responses to being in allopatry or sympatry. Simberloff et al (2000) found sexual dimorphism to be greater for mongooses populations in allopatry compared to populations in sympatry with a congener because the absence of a competitor likely allowed an increased exploitation of resources. My findings support the prediction that sexual dimorphism should be greater in allopatry. Whether the observed morphological patterns in this system are due to genetic difference or phenotypic plasticity remains unknown and a next step to better understand what maintains body shape variation in allopatric populations.

COMPARING MULTIPLE TRAITS

Although theory predicts that co-occurring populations of different species should show significant phenotypic divergence relative to isolated populations, it is not clear which traits should diverge and if some traits should show greater levels of divergence than others. Streelman and Danley (2003) predicted a sequential pattern of trait divergence among vertebrates with overlapping distributions, with traits associated with habitat use diverging first (i.e. diet or foraging behavior), followed by morphological divergence, and finally divergence in traits related to communication. Their rationale for these predictions is that competition first drives species to utilize different habitat resources. Secondary morphological specializations related to resource acquisition should then evolve within habitats. Finally, sensory communication traits reinforcing species recognition or evolving with mate choice should evolve. In this study I do not

test if trait divergence follows a predicted order; however, I do identify two traits that show divergence in populations that occur in sympatry: life history and body shape. Following Streelman and Danley's prediction these two traits may be greatly subject to divergence, but no predictions are made for how males and females should each respond or if they should respond differently. An important element of my study is that I explore size at maturity for both males and females and compare the amount of sexual dimorphism between populations. Sex-specific divergence is predicted to arise from interactions between environmental gradients and sex-specific morphology or behavior (Hendry et al., 2006). By comparing both life history traits and body shape, we find evidence to support this prediction, particularly in that greater amounts of sexual dimorphism are found in allopatry compared to sympatry. Both traits show significant divergence in sympatric compared to allopatric populations, but there is a difference in the response between males, who show no differences in life history strategies between sympatric and allopatric populations, and females, who do show differences. In other words, the responsiveness of sexual dimorphism to environment factors adds further support that males and females may occupy separate niches (Butler, Sawyer, & Losos, 1996) and respond differently to the presence of a potential competitor.

While life history strategies and body shape divergence provide valuable insight to the nature of sympatric environments, a next approach to accompany phenotypic trait divergence is to compare communication patterns in allopatric and sympatric populations. For example, preliminary work suggests that spotting pattern differences between species might be used as a species recognition cue in this system (Scott, unpubl. data). Traits related to communication patterns are often subject to selection in sympatric environments (Benedix, 1991; Gabor and Ryan, 2001; Lemmon, 2009) and provide additional insight to the unique adaptations for species recognition each sex evolves in sympatry.

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Figure Legends

Figure 1. Geographic sampling localities of *Poeciliopsis baenschi* included in this study. Filled squares identify locations where *P. baenschi* is the only livebearing fish species present at a collection site (allopatric populations); triangles identify locations where *P. baenschi* co-occurs with the congeneric species *P. turneri* (sympatric populations).

Figure 2. Comparisons of life history traits of allopatric and sympatric populations of *P. baenschi*: (A) male size at maturity; (B) female size at maturity; (C) number of broods; (D) reproductive allotment per brood; (E) number of offspring; and (F) size of offspring. Values presented are least square means from the general linear model analyses (± 1 SE) (see text).

Figure 3. Characterization of morphological variation in body shape in *Poeciliopsis baenschi* comparing allopatric and sympatric populations. Relative warp (RW) scores (± 1 SE) for males and females from each population type are plotted along the first two relative warp axes (axes units are arbitrary) showing differences in body shape. The first two relative warps account for 90.8% of the total variation in body shape; RW2 is amplified in this figure by a factor of three to show differences among sexes. Deformation plots (3x) are presented for males and females from each population type; dotted lines connect RW values to their associated deformation plots.

Table 1. List of GPS coordinates and ecological stream measurements for each collection site. Collection sites 1-7 are allopatric; sites 8-15 are sympatric. Collection numbers correspond to those found in Figure 1.

		GPS coordinates		Stream characteristics		
Habitat	**Collection**	**Latitude**	**Longitude**	**Flow rate (m/s)**	**Temperature °C**	**pH**
Sympatric	1	19.701°N	104.598°W	--	26.8	--
	2	19.676°N	104.576°W	0.01	28.3	6.5
	3	19.622°N	104.548°W	0.01	33.8	6.8
	4	19.529°N	104.582°W	0.01	31.0	7.0
	5	19.495°N	104.672°W	0.14	31.0	6.4
	6	19.501°N	104.767°W	0.01	31.5	6.5
Allopatric	7	20.315°N	105.320°W	--	23.2	--
	8	18.956°N	103.945°W	0.01	25.5	6.5
	9	19.254°N	104.174°W	--	29.0	6.7
	10	19.272°N	104.295°W	0.24	29.0	7.0
	11	19.203°N	104.336°W	0.01	26.8	6.8
	12	19.745°N	104.158°W	--	27.0	6.8
	13	19.194°N	103.836°W	0.38	29.3	6.8
	14	18.956°N	103.945°W	0.35	27.3	7.0
	15	18.977°N	103.698°W	0.01	28.3	6.5

(--) data not available

Table 2. Summary of life-history traits from 12 populations of *Poeciliopsis baenschi*; values for number of broods, reproductive investment, number of offspring, and size of offspring are adjusted least square mean values from the general linear models described in text. Collection number corresponds to those in Figure 1.

Type of habitat	Collection	*n* males	Male size at maturity (mm)	*n* females[a]	Minimum size of mature females (mm)	Number of broods	Reproductive Investment per brood (mg)	Number of offspring	Size of offspring (mg)
Sympatric	1	50	20.0	40	20	1.2	3.42	2.9	1.28
	2	50	20.1	29	20	1.2	3.62	3.3	1.27
	3	42	20.3	32	24	1.2	2.56	2.6	1.03
	4	43	18.3	31	20	1.3	2.38	2.4	1.09
	5	39	19.1	24	22	1.2	4.56	4.4	1.20
	6	39	19.5	31	20	1.3	2.19	2.7	0.90
Allopatric	7	16	22.5	55	20	1.1	5.29	4.1	1.47
	8	51	19.7	33	20	1.2	4.15	4.2	1.07
	11	51	18.6	29	18	1.2	4.30	5.1	0.92
	12	50	18.1	30	18	1.2	1.87	2.7	0.78
	14	50	18.6	31	18	1.5	3.70	7.2	0.54
	15	51	19.1	34	18	1.4	3.93	5.4	0.86

[a] sample sizes indicate the number of mature females observed out of the total number of females dissected

Table 3. Statistical results for six life history traits from 12 populations of *P. baenschi* evaluating the effects of sympatric or allopatric habitat on life history. Size at maturity was evaluated using a one-way ANOVA; number of broods evaluated by a logistic regression; reproductive investment, number and size of offspring evaluated using an ANCOVA.

Response Variable	**Effect**	***df***	***F***	***P***
size at maturity	males	1	0.011	0.91
	females	1	10.63	0.02
number of broods	habitat	1, 385	2.51	0.11
	female mass	1, 385	25.64	<0.001
	female mass x habitat	1, 385	1.83	0.17
reproductive investment	habitat	1, 198	9.98	0.002
	female mass	1, 307	114.25	<0.001
	female mass x habitat	1, 307	4.75	0.03
number of offspring	habitat	1, 135	13.55	<0.001
	female mass	1, 395	175.93	<0.001
	female mass x habitat	1, 395	4.6	0.03
size of offspring	habitat	1, 147	1.7	0.19
	female mass	1, 395	0.26	0.60
	female mass x habitat	1, 395	5.01	0.02

Table 4. Results from mixed model MANOVA effects on body shape variation. Habitat (allopatric or sympatric), sex and order were main effects; population was evaluated as a random effect. The 'order' term represents the order of the relative warps; significant results with the order term are of most interest to this study (see text).

Effect	***df***	***F***	***P***
Habitat	1, 689	1.9	0.16
Sex	1, 681	1.0	0.30
Order	10, 2869	20.7	<0.001
Habitat x Sex	1, 681	0.3	0.60
Habitat x Order	10, 2869	34.2	<0.001
Sex x Order	10, 2868	1,468	<0.001
Habitat x Sex x Order	10, 2868	4.2	<0.001

Figure 1.

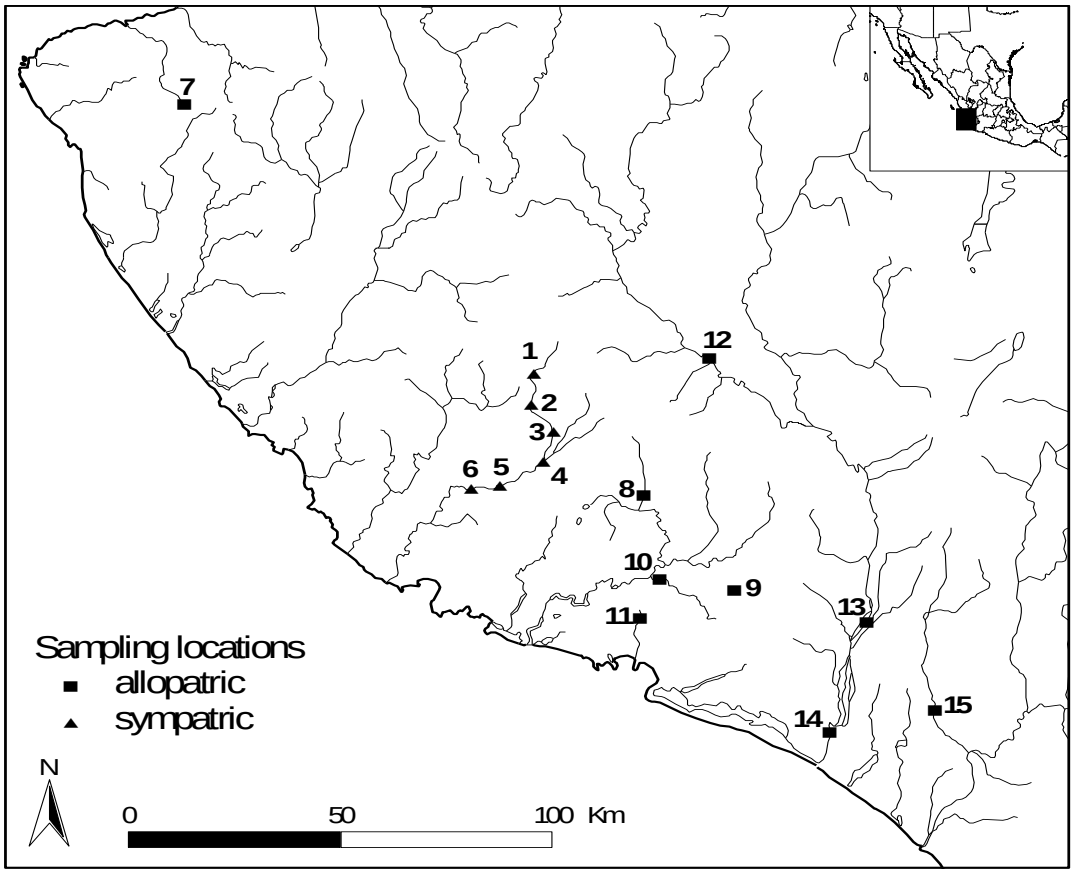

7
1
2
3
6
5
4
12
8
10
9
11
13
14
15
Sampling locations
allopatric
sympatric
N
0
50
100 Km

Figure 2.

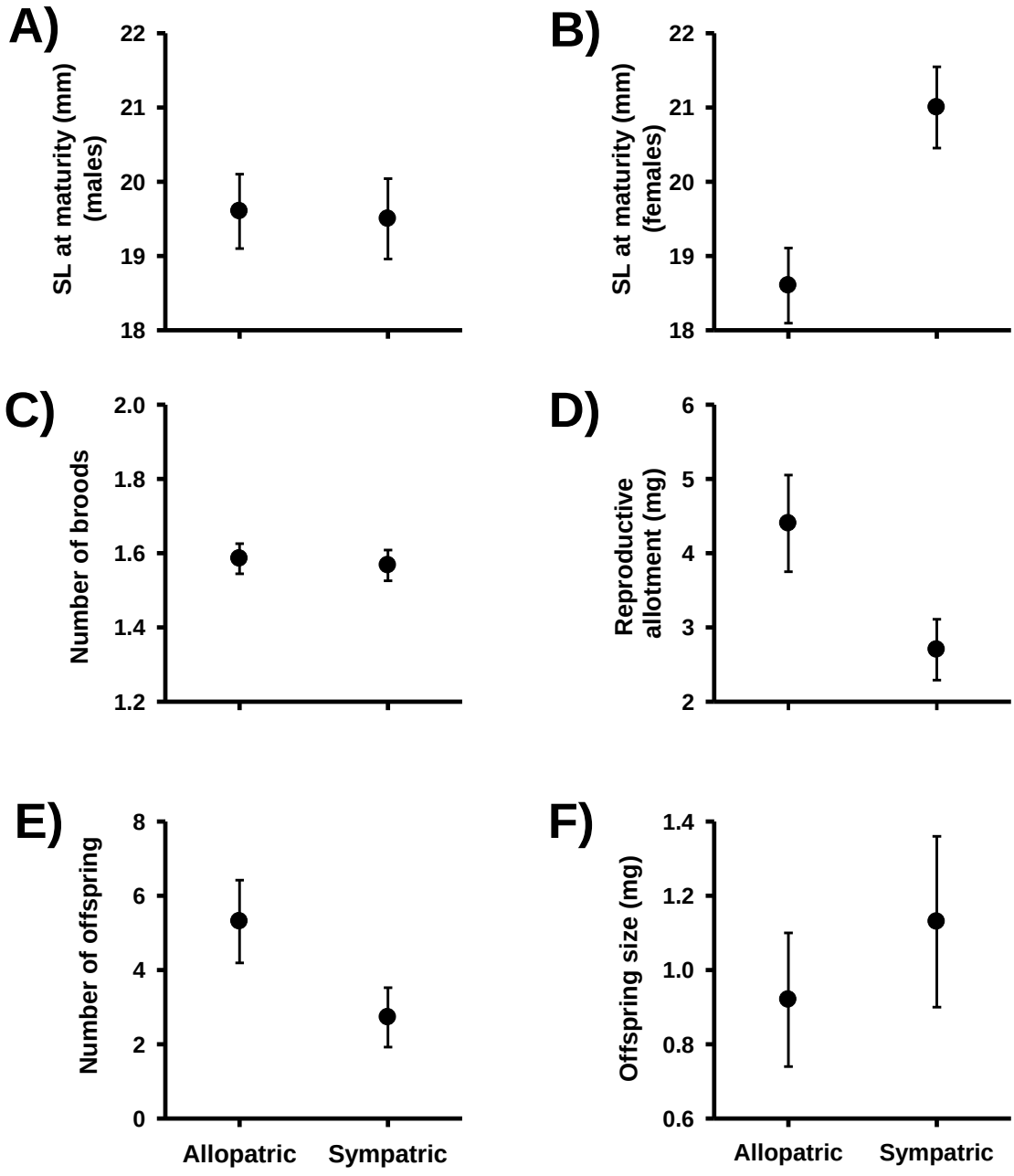
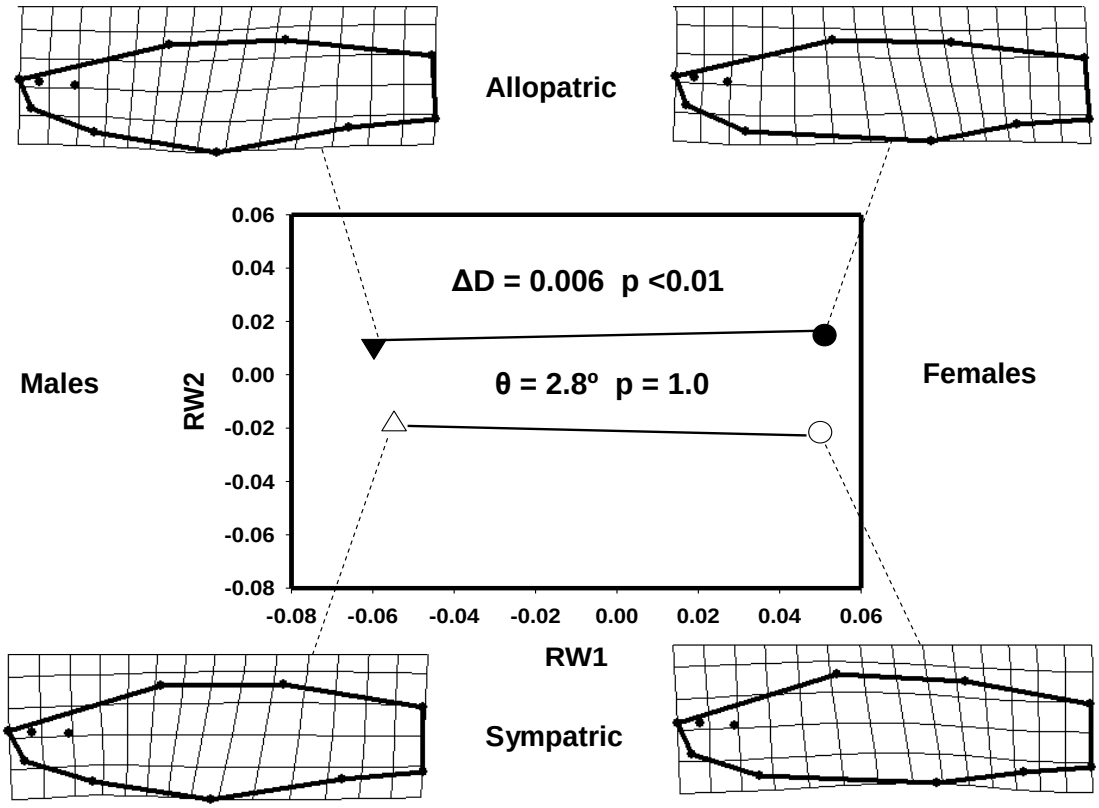

A)
SL at maturity (mm) (males)
22
21
20
19
18
B)
SL at maturity (mm) (females)
22
21
20
19
18
C)
Number of broods
2.0
1.8
1.6
1.4
1.2
D)
Reproductive allotment (mg)
6
5
4
3
2
E)
Number of offspring
8
6
4
2
0
Allopatric
Sympatric
F)
Offspring size (mg)
1.4
1.2
1.0
0.8
0.6
Allopatric
Sympatric

Figure 3.


Allopatric
Males
Females
Sympatric
ΔD = 0.006 p <0.01
θ = 2.8° p = 1.0
RW2
RW1
0.06
0.04
0.02
0.00
-0.02
-0.04
-0.06
-0.08
-0.08 -0.06 -0.04 -0.02 0.00 0.02 0.04 0.06