Lifetime Fitness, Sex-Specific Life History, and the Maintenance of a Polyphenism

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ABSTRACT: Polyphenisms—alternative morphs produced through plasticity—can reveal the evolutionary and ecological processes that initiate and maintain diversity within populations. We examined lifetime fitness consequences of two morphs in a polyphenic population of Arizona tiger salamanders using a 27-year data set with 1,317 adults and 6,862 captures across eight generations. Larval salamanders develop into either an aquatic paedomorph that retains larval traits and stays in its natal pond or a terrestrial metamorph that undergoes metamorphosis. To evaluate the adaptive significance of this polyphenism, we compared lifetime reproductive success of each morph and assessed how life-history strategies and spatiotemporal variation explained fitness. We found sex-specific differences in lifetime fitness between morphs. For males, paedomorphs had more reproductive opportunities than metamorphs when we accounted for the potential mating advantage of larger males. For females, in contrast, metamorphs had higher estimated egg production than paedomorphs. Life-history strategies differed between morphs largely because the morphs maximized different ends of the trade-off between age at first reproduction and longevity. Spatiotemporal variation affected larval more than adult life-history traits, with little to no effect on lifetime fitness. Thus, environmental variation likely explains differences in morph production across time and space but contributes little to lifetime fitness differences between morphs and sexes. Our long-term study and measures of lifetime fitness provide unique insight into the complex selective regimes potentially acting on each morph and sex. Our findings motivate future work to examine how sex-specific selection may contribute to the maintenance of polyphenism.

Keywords: lifetime reproductive success, fitness, life history, polyphenism, environmental heterogeneity, *Ambystoma*.

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Introduction

Understanding the factors that promote and maintain diversity within a population is a major goal in evolutionary biology because it provides insights into how populations can adapt to their environments. Some of the most dramatic examples of diversity within populations result from polyphenism, which occurs when a single genotype can produce alternative, discrete phenotypes under different environmental conditions (Mayr 1963; West-Eberhard 1989, 2003; Pfennig et al. 2010; Simpson et al. 2011). The puzzle lies in determining what conditions maintain a polyphenism rather than a single phenotype, a genetic polymorphism, or the evolution of distinct species. Theory predicts that environmental heterogeneity that alters selection across time or space could favor the initial evolution and maintenance of plasticity (Levene 1953; Levins 1968; West-Eberhard 1989, 2003; Wilson 1989; Moran 1992; Gross 1996; Roff 1996; Sultan and Spencer 2002).

Determining how selection maintains polyphenism requires measuring the fitness consequences of each alternative phenotype. Selection should favor the maintenance of a polyphenism if each morph has higher fitness on average than the other morph in a particular environment (West-Eberhard 1989). Many agents of selection can contribute to the production and/or maintenance of polyphenism, including variation in resource use, competitor density, relative growth rates, presence of predators or parasites, and frequency or density of each morph (Pfennig et al. 2010; Simpson et al. 2011). Differences in fitness between the sexes within each morph could also contribute to maintaining a polyphenism. For instance, in sand crickets (*Gryllus firmus*), each sex experienced different costs as flightless or flight-capable morphs, which, in combination with a genetic correlation between the sexes for wing dimorphism, contributed to the maintenance of both morphs (Roff and Fairbairn 1993). Multiple sources of selection can also interact to produce or maintain a polyphenism.

For example, selection could vary within an individual's lifetime across developmental stages or between different environments (Schluter et al. 1991; Mojica and Kelly 2010). The strength or direction of selection could also differ between generations in temporally variable environments (Levins 1968; Caswell 1983; Siepielski et al. 2009). Many studies examine a snapshot of selection by measuring fitness at one life stage, in one generation, or using one fitness proxy (Kingsolver et al. 2001). However, the most comprehensive understanding of how selection contributes to the production and maintenance of polyphenism requires measuring fitness throughout organisms' lifetimes and across generations (Lande and Arnold 1983; Arnold and Wade 1984; Endler 1986; Clutton-Brock 1988, 1991).

Alternative morphs may attain environment-specific fitness payoffs through different life-history strategies (i.e., correlated suites of traits that involve growth, reproduction, and life span; Lively 1986; Stearns 1989; Roff 1996; Kivelä et al. 2013). Within each morph, life-history traits might evolve in concert because a change in one trait can affect developmentally or functionally related traits (Moczek et al. 2011). Between morphs, distinct selection regimes in environments exploited by each morph may favor differences in the presence, direction, or strength of trait correlations. For instance, in spadefoot toads, diet-induced changes in tadpole gut morphology in carnivore morphs are correlated with altered foraging behavior and mouth structures (Pfennig and Murphy 2000). Trait correlations can also involve trade-offs. A common trade-off occurs between rate of development and size at maturity, where individuals that develop faster are often smaller at maturity (Stearns 1989). Examining differences in life-history strategies between morphs provides insight into fitness consequences for each morph throughout the life cycle as well as how alternative life-history strategies could contribute to the maintenance of polyphenism.

Here we compared lifetime fitness consequences and underlying life-history strategies of two morphs in a population of long-lived, polyphenic tiger salamanders. This population is facultatively paedomorphic; larvae develop into one of two environmentally induced adult morphs. Aquatic paedomorphs retain larval traits, such as gills, while terrestrial metamorphs undergo metamorphosis. Previous work on this population has identified that morph production is determined by intraspecific competitor density, size structure, larval growth rate, and larval size and condition, all of which vary across space and time (Whiteman et al. 2012). In this study, we evaluated the adaptive significance of this polyphenism using estimates of fitness and life history from a 27-year data set. We expected that distinct selective regimes act on each morph due to differences in development (metamorphosing or not) and adult habitat (terrestrial or aquatic). First, we compared measures of lifetime reproduction between the morphs and sexes to understand how fitness consequences across their life spans could contribute to the maintenance of polyphenism. Second, we tested for differences between the morphs and sexes in life-history traits and the correlations among life-history traits to evaluate how life-history strategies affected lifetime fitness. Last, we tested the hypothesis that environmental heterogeneity could maintain a polyphenism by comparing fitness consequences and life-history traits of each morph across larval ponds and cohorts, which are two major sources of spatiotemporal variation in competitor density, prey availability, and abiotic factors (Whiteman et al. 1994, 2012; Wissinger et al. 2003; Whiteman and Wissinger 2005).

Methods

Study Population

We studied a population of Arizona tiger salamanders (*Ambystoma mavortium nebulosum*, formerly *Ambystoma tigrinum nebulosum*; Shaffer and McKnight 1996; Irschick and Shaffer 1997) located in western Colorado at the Mexican Cut Nature Preserve, which is property of the Nature Conservancy (3,640 m asl; 39.02°N, 107.06°W). This subalpine site contains an array of more than 24 ponds, which are isolated from other ponds by several kilometers, limiting migration in or out of this watershed (Whiteman et al. 1996; see a map of the ponds in Wissinger et al. 2003). Salamanders breed, develop, and forage in these ponds during the ice-free summer months (usually June–September; Wissinger and Whiteman 1992; Whiteman and Wissinger 2005). Long-term monitoring of this population started in 1988 and is ongoing. Larval and adult salamanders were individually marked with passive integrated transponder tags or toe clips. Salamanders were captured using dip nets or by hand, and snout-vent length (SVL), total length, mass, maturity, sex, evidence of breeding condition (described below), and capture date and pond were recorded. Salamanders were returned to the pond in which they were captured. Sampling across ponds occurred almost daily between June and August, and many salamanders were captured multiple times (range: 2–5 captures) in 1 year. Previous mark and recapture estimates suggest that over 95% of salamanders in this population have been captured and recorded in these surveys (Whiteman 1997).

The Mexican Cut population of tiger salamanders are facultatively paedomorphic, and larvae can develop into one of two adult morphs. Paedomorphs retain their larval characteristics and remain in their natal ponds while attaining sexual maturity. In contrast, metamorphs transform and disperse into the terrestrial environment (Moore and Whiteman 2016); they then return to the ponds during the ice-free season to mate and/or forage in both breeding and nonbreeding years (Wissinger and Whiteman 1992; Whiteman et al. 1994, 1996). Morph production depends on relative larval body size and

condition as well as population density within years and in previous years (Whiteman 1994; Whiteman et al. 2012) and is likely mediated by thyroid hormone (Voss et al. 2012). Previous work by Whiteman et al. (2012) has established the following patterns for how larval body condition correlates with morph production. A small number of larvae with the highest condition tend to develop into large paedomorphs, which have a competitive advantage over smaller individuals. Larvae in moderate to high condition can develop into paedomorphs or metamorphs but typically metamorphose. Due to short growing seasons, larvae often do not reach the minimum size necessary for metamorphosis until their third summer (2 years old). Larvae that reach this size threshold and metamorphose avoid competition from large paedomorphs. Larvae with the lowest condition, which occur most often in high-density populations, are more likely to become paedomorphs than metamorphs but take several more years to sexually mature.

In this study, we analyzed data collected between 1988 and 2015 from salamanders with known cohorts. We used individuals with hatching dates between 1988 and 2001, which resulted in 27 years of data for the oldest cohort and 14 years of data for the youngest cohort. For salamanders surviving to adulthood, the maximum life span was 26 years, and the average was 10 ($\pm$ 4 SD). Thus, this analysis encompassed the entirety or majority of each salamander's lifetime and included 1,317 adults with 6,862 total captures.

Measures of Lifetime Fitness

We calculated two types of metrics of reproductive success: number of lifetime reproductive opportunities (both sexes) and condition-weighted estimates of lifetime reproduction for each sex. We calculated condition by dividing mass by SVL (Whiteman et al. 2012). A condition metric should predict fitness more precisely than body length or body mass because it separates body mass explained by structural size from that explained by nutrient reserves (e.g., Schamber et al. 2009). Our condition metric of mass divided by SVL predicts total fat reserves better than ordinary least squares (OLS) residuals in tiger salamanders (box B1, available online). For males, condition-weighted number of reproductive opportunities accounts for the potential advantage of larger males gaining access to females. For females, estimated lifetime egg production was based on the correlation between body condition and egg production. We used these measures of mating opportunities because our capture data did not provide sufficient information to detect the number of successful matings for each individual; we could not observe all mating events, noninvasively count each female's eggs, or determine parentage. Our fitness proxies, however, provide important insight into reproductive potential of salamanders of each sex and morph. To count the number of lifetime reproductive opportunities, we considered a female to have a reproductive opportunity when she was in breeding condition, evidenced by a swollen cloaca. Females are energetically constrained to a single breeding event each year (Whiteman 1997; Petranka 1998). A male had a reproductive opportunity when he was in breeding condition (swollen cloaca) and captured during the first 30 days of the breeding season. Later in the season, very few females are gravid, and any males that develop or maintain a swollen cloaca should be unlikely to mate (fig. B1; figs. B1, B2, D1 are available online).

Some males may mate multiple times, while others do not mate due to male-male competition and female choice (Whiteman 1997; Whiteman et al. 1999). Thus, among males in reproductive condition each year, mating success likely varies substantially. To estimate the potential for reproductive skew in mating success in this population, we calculated the operational sex ratio (OSR, proportion of reproductive males to females; Emlen and Oring 1977) in each year and pond when there were at least five males and five females captured (male range = 6–250; female range = 5–58). We used measures of OSR to justify whether it was appropriate to account for the potential mating advantage of larger males in our analyses. Higher OSR predicts greater variance in male mating success (Emlen and Oring 1977; Janicke and Morrow 2018). Also, previous work in Eastern tiger salamanders found that males with longer bodies had greater access to females (Howard et al. 1997). Thus, larger males of our focal species may be more likely to have multiple mates relative to smaller males. To account for the potential mating advantage of larger males, we weighted each male's reproductive opportunities by his relative body condition. To calculate condition-weighted reproductive opportunities, we standardized each male's condition each year he was in reproductive condition using the distribution of all males in reproductive condition that year. Within each year, we standardized condition to have a mean and standard deviation of one. We used a male's standardized condition to weight his reproductive opportunities as follows: a male with average condition for that year would have one reproductive opportunity, a male with lower condition than the average would have less than one reproductive opportunity with a lower limit of zero, and a male with higher condition than the average would have more than one reproductive opportunity with no upper bound. We weighted reproductive opportunities using the selection coefficient estimate of 0.2 for selection on mating traits from a meta-analysis by Kingsolver et al. (2012). Applying this estimate to our analyses, a male with a standardized condition one standard deviation greater than the standardized mean of one would have a weighted reproductive opportunity of 1.2. We summed a male's condition-weighted reproductive opportunities across his lifetime.

For females, absolute body size correlates with clutch size (fig. B2), so we used body condition in reproductive years to

estimate lifetime egg production. First, we calculated the regression between measured clutch sizes and adult condition for a subset of 86 females (fig. B2). We then used the intercept and slope of the regression line to estimate egg production per reproductive opportunity for each female using her measured average adult condition during reproductive years (i.e., estimated egg production per reproductive opportunity = intercept + slope × average adult condition during reproductive years). Last, to calculate estimated lifetime egg production, we multiplied each female's estimated egg production per reproductive opportunity by her total number of reproductive opportunities.

Measures of Life-History Traits

We calculated the following life-history traits: longevity, age at first reproduction, adult condition (in reproductive and nonreproductive years), and larval condition. We calculated longevity given an individual's cohort and their known death or final capture year. For most salamanders, final capture year was the assumed date of death; therefore, we have underestimated longevity, and any detected morph differences are likely conservative. Age at first reproduction was calculated as the age that each salamander had its first reproductive opportunity. Our data likely capture the actual minimum age of first reproduction, but age at first reproduction could be overestimated for some individuals because not all salamanders were caught every year. We averaged adult condition across all adult captures for each individual. We used larval condition in the third summer of development (2 years old), which is the year in which most larvae develop into a metamorph or paedomorph (Whiteman et al. 2012). When larvae were captured multiple times in their third summer, we averaged measures of larval condition.

Measures of Environmental Heterogeneity

In this study, we examined two major sources of spatiotemporal variation: larval pond and cohort (i.e., birth year). We expected that spatiotemporal variation would affect fitness of each morph for two primary reasons: first, competitor density varies across ponds and years and strongly predicts morph production (Whiteman and Wissinger 2005; Whiteman et al. 2012), and second, paedomorphs stay in their larval ponds throughout their lifetimes while metamorphs disperse into the terrestrial environment after the larval period. The effects of larval pond and cohort may differ between the sexes given potential sex differences in fitness within each morph and environmental variation across time and space (Whiteman 1997; Whiteman et al. 2012). We included all sampled ponds and cohorts except those that produced two or fewer adults across the 27 years of observation, which resulted in six ponds and eight cohorts (fig. 1). Model selection and conclusions were the same with or without these low-producing ponds and cohorts. Larval survival to adulthood was low in some ponds and years due to intraspecific effects, including cannibalism and density-dependent growth (Whiteman and Wissinger 2005; Wissinger et al. 2010; Whiteman et al. 2012).

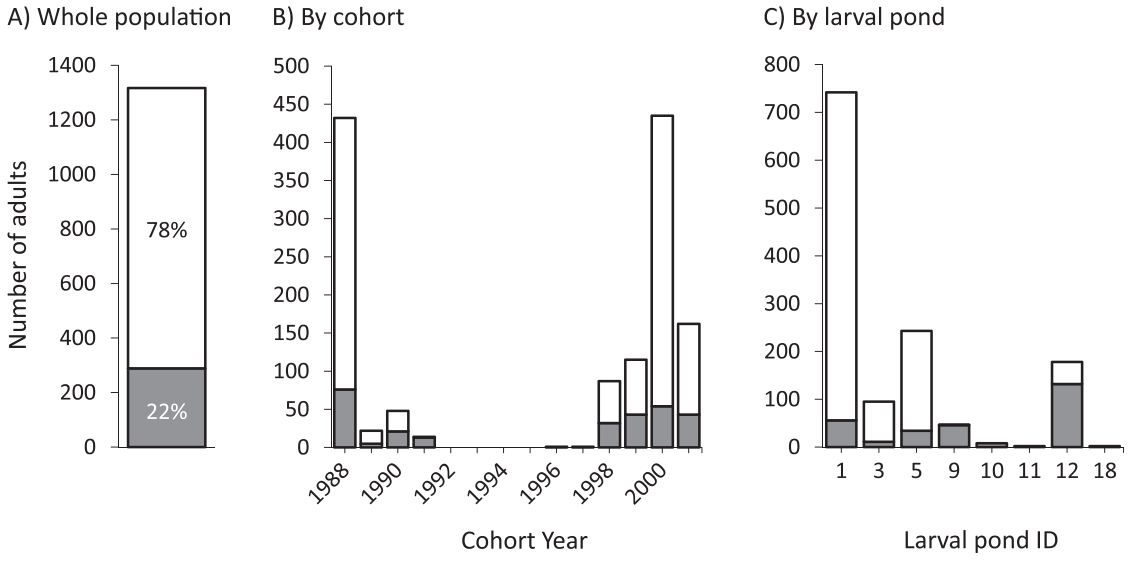

Figure 1: Total number of adults of each morph in the population (*A*), in each cohort (*B*), and from each larval pond (*C*). Paedomorphs are shown in white; metamorphs are shown in gray. Cohorts 1992–1995 and larval pond numbers absent from the sequence 1–18 produced no hatchlings that survived to adulthood. In generalized linear mixed models, the eight cohorts included were 1988, 1989, 1990, 1991, 1998, 1999, 2000, and 2001, and the six ponds included were 1, 3, 5, 9, 10, and 12.

Statistical Analysis

We used generalized linear mixed models (GLMMs) to test for differences in lifetime reproduction and life-history traits between adults of each morph, sex, pond, and cohort. Because of the potential for correlations among variables in our models, we tested for multicollinearity using the variance inflation factor (VIF). For all variables, VIF values were all less than two, which indicated that multicollinearity was unlikely to bias our results (Petraitis et al. 1996). We performed GLMM analyses using SAS (SAS Institute, Cary, NC). We used PROC GLIMMIX, which applies maximum likelihood estimation and a residual degrees of freedom method when a model contained no random effects or residual pseudolikelihood estimation and a containment degrees of freedom method when the model included random effects. We reported estimates of model terms as follows: mean estimate (95% confidence interval [CI]). Data are available from the Dryad Digital Repository: https://dx.doi.org/10.5061/dryad.52kd8tg (Lackey et al. 2019).

To test for differences in lifetime reproduction between morphs and sexes, we analyzed number of reproductive opportunities and lifetime estimated egg production as response variables in separate models. These models included life-history traits and two-way interactions between life-history traits, morph, and sex to evaluate the relative importance of each variable (for model effects, see table A1; tables A1, A2, C1, C2 are available online). Using this approach, we tested effects of morph and sex after controlling for variation in lifetime fitness explained by life-history traits. We selected models using backward elimination with Akaike's information criterion. We modeled reproductive opportunities using a GLMM with a Poisson distribution and logit link function.

To test for differences between morphs and sexes in life-history traits and the relationships among life-history traits, we analyzed a series of GLMMs with each life-history trait (i.e., longevity, age at first reproduction, adult condition, and larval condition) as the response variable. Explanatory variables included morph, sex, the interaction of morph and sex, other life-history traits that could contribute to the response variable, and two-way interactions of each life-history trait with morph and sex as explanatory variables. For example, we analyzed longevity as the response variable with the following explanatory variables as fixed effects: age at first reproduction, adult condition, larval condition, morph, sex, and their two-way interactions. We also included larval pond and cohort as random effects (table A1). We modeled longevity and age at first reproduction using logistic regression with a Poisson distribution and logit link function. Adult and larval condition were normally distributed, so we used linear regression with a normal distribution.

We also used path analysis using maximum likelihood (Shipley 2000) to test hypothesized relationships among life-history traits as well as the extent to which life-history traits predicted our measure of lifetime reproductive success for both sexes (i.e., number of reproductive opportunities). Path analysis allowed us to distinguish between direct and indirect relationships among variables, which was not possible with multiple regression. We tested three hypothesized path models in each morph and sex separately (fig. 2*A*). Hypotheses were based on life-history theory (Stearns 1989), findings and expectations for facultatively paedomorphic populations (Whiteman 1994; Denoël et al. 2005), and previous results from this population (Whiteman 1997; Whiteman et al. 2012). We made the following predictions for relationships among life-history traits. Larval condition could have carryover effects to adulthood, resulting in positive or negative relationships with adult condition, age at first reproduction, longevity, and number of reproductive events (Semlitsch et al. 1988; Scott 1994; De Block and Stoks 2005; Crean et al. 2011; Schmidt et al. 2012; Earl and Semlitsch 2013; Green and Bailey 2015; Müller et al. 2016). Age at first reproduction and adult condition could be correlated due to a trade-off between reproduction and growth or because reproduction requires a minimum adult size (Roff 1992; Stearns 1992). Age at first reproduction could also affect longevity because earlier breeding is often correlated with shorter life spans (Stearns 1992; Ricklefs 2010). Adult condition could affect longevity if a trade-off exists between growth and survival (Metcalfe and Monaghan 2003). Last, age at first reproduction, adult condition, and longevity could influence the lifetime number of reproductive opportunities (Stearns 1976, 1992; Clutton-Brock 1988).

Our three hypothesized models shared the same structure and differed in whether individual paths were excluded (i.e., modeled with the path coefficient fixed at zero). Models differed in whether they predicted that larval condition affected longevity, number of reproductive opportunities, or neither, with the expectation that carryover effects from the larval to adult stage could vary between morphs due to differences in development. We tested model fit using the maximum likelihood χ^2 statistic, which tests whether the covariance structure implied by the path model is statistically equivalent to the observed covariance structure (Mitchell 1992; Shipley 2000). Using multigroup, nested modeling approaches (Shipley 2000), we tested whether the same model structure could be applied to each morph and sex, and we tested whether the relationships among variables (i.e., the life-history trait relationships) differed among groups. Path analysis excludes any observation with incomplete data (e.g., missing age at first reproduction). Our analysis included 166 paedomorphic males, 127 paedomorphic females, 91 metamorphic males, and 70 metamorphic females. We used SAS procedure PROC CALIS.

To test for effects of spatiotemporal variation, we included random effects for larval pond and cohort for each of the

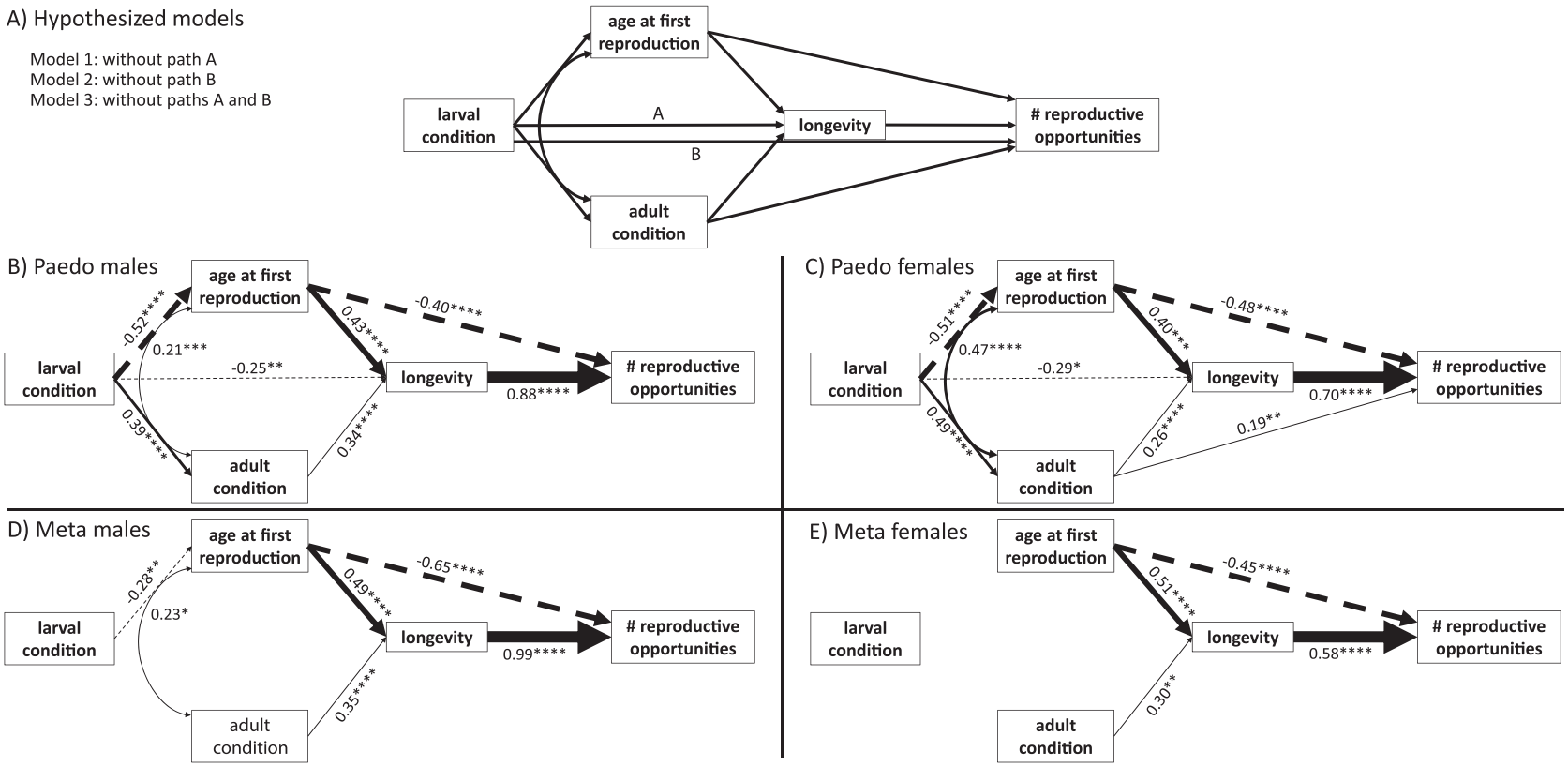

Figure 2: Path analysis models. The three hypothesized models (*A*) and the strength and direction of paths supported by data in the best-fit model (model 2) for each morph and sex: paedomorphic males (*B*), paedomorphic females (*C*), metamorphic males (*D*), and metamorphic females (*E*). Standardized path coefficients are shown next to each arrow, and arrow thickness corresponds to the strength of the path coefficient. Solid arrows depict positive relationships, and dashed arrows show negative relationships. Single-headed arrows are directional relationships, while double-headed arrows represent correlations. Only significant relationships with path coefficients greater than 0.2 are shown, and asterisks show the significance of each path coefficient: $^{*}P < .5$; $^{**}P < .01$; $^{***}P < .001$; $^{****}P < .0001$.

GLMMs described above. Larval pond and cohort capture spatial and temporal variation, respectively (fig. 1). We modeled random effects as G-side effects, which treat each random effect as a covariate in the model. Thus, we could estimate the effect of larval pond and cohort overall on metrics of lifetime fitness and life-history traits. Also, we could estimate the effect of each of the six ponds and eight cohorts on our response variables given that the levels of each effect were considered to be a random sample of all possible levels (Robinson 1991; Houslay and Wilson 2017). In contrast, an R-side random effect would estimate the residual error accounted for in the model by that term. We excluded a random effect if the model would not converge (table A2).

Results

Number and Frequency of Adults of Each Morph

Across all cohorts and ponds, there were significantly more paedomorphs produced than metamorphs (paedomorphs: 1,028 adults, 78%; metamorphs: 289 adults, 22%; $\chi^2 = 414.67$, df $= 1$, $P = .013$; fig. 1*A*). The relative frequency of each morph produced differed across larval ponds ($\chi^2 = 571.38$, df $= 5$, $P < .0001$; fig. 1*B*) and cohorts ($\chi^2 = 108.86$, df $= 7$, $P < .0001$; fig. 1*C*).

Comparing Lifetime Reproduction between Morphs and Sexes

Lifetime reproductive opportunities ranged from zero to 10, with 75% of adults having zero or one reproductive opportunity (fig. 3*A*, 3*B*). In the following models, we present morph differences in lifetime fitness using two metrics of reproductive success for each sex: (1) a count of reproductive opportunities for males and females and (2) condition-weighted estimates of reproductive opportunities for males and egg production for females. Our models included life-history traits; thus, morph effects were those remaining after accounting for variation explained by life history. When we analyzed lifetime reproductive success of both sexes together, the majority of variation in number of reproductive opportunities (i.e., number of years in reproductive condition in a lifetime) was explained by longevity ($F_{1, 257} = 78.15$, $P < .0001$) and age at first reproduction ($F_{1, 257} = 28.11$, $P < .0001$) but not morph ($F_{1, 257} = 1.29$, $P = .26$).

To estimate the potential for reproductive skew and male competition for access to females, we measured the OSR. Across all years and ponds of this study, OSR was 0.39 on average, which is approximately three males per female (SD $=$ 0.57; range $=$ 0.053–2.33). When we accounted for potentially higher mating success of larger males, we found that paedomorphic males had significantly more reproductive opportunities than metamorphic males independent of differences in life-history traits (paedomorphs: 0.35 [95% CI: 0.22–0.55]; metamorphs: 0.18 [0.10–0.31]; $F_{1, 370} = 22.63$, $P < .0001$; fig. 3*C*). In contrast to the advantage of paedomorphic males in condition-weighted reproductive opportunities, metamorphic females produced more eggs per lifetime than paedomorphic females on average after accounting for variation explained by life-history traits (paedomorphs: 65.70 [60.40–71.46]; metamorphs: 199.25 [183.67–216.16]; $F_{1, 77} = 662.85$, $P < .0001$; fig. 3*D*). Morph differences in estimated lifetime egg production remained even when we excluded statistically influential values above 1,000 eggs per lifetime (paedomorphs: 91.99 [84.06–100.68]; metamorphs: 177.40 [162.26–193.95]; $F_{1, 74} = 178.60$, $P < .0001$). These results showed a potential advantage for paedomorphic males and metamorphic females over the other sex within each morph, which motivated tests for sex ratio differences between the morphs. Across all ponds and cohorts, sex ratios did not differ between morphs (table 1). However, earlier cohorts with sex ratio differences between morphs showed biases toward metamorphic females and paedomorphic males, which was consistent with the pattern of sex-specific fitness benefits within morphs (table 1). In contrast, later cohorts with sex ratio differences between morphs were biased toward paedomorphic females (table 1). This change across cohorts in sex ratio biases contributed to the lack of sex ratio differences between morphs when analyzed across all cohorts. Differences in reproductive success between morphs and sexes were not explained by morph differences in number of captures. Capture frequency did not differ between morphs and sexes (Kruskal-Wallis $\chi^2 = 3.98$, df $= 3$, $P = .26$).

Comparing Life-History Strategies between Morphs

We evaluated life-history strategies between morphs and sexes by comparing relationships among life-history traits using path analysis and regression. We tested model fit for three hypothesized path models (fig. 2*A*). The structure (i.e., the paths connecting the variables) of model 2 was the best fit for the morphs and sexes combined ($\chi^2 = 9.71$, df $=$ 20, $P = .97$). A P value less than .05 suggests that the data are inconsistent with the hypothesized model. Model 2 excluded the causal relationship between larval condition and number of reproductive opportunities (fig. 2*A*). Model 1 was an acceptable fit ($\chi^2 = 9.71$, df $= 20$, $P = .49$), while model 3 was a poor fit ($\chi^2 = 30.4$, df $= 20$, $P = .064$). For model 2, we then used nested model χ^2 tests (Shipley 2000) to determine whether the strength and direction of each path were the same across all morphs and sexes. Significant P values indicate that a path with a free parameter determined by the data for each morph and sex was a better fit than a path constrained to a shared value across all morphs and sexes. We found that all paths differed among the morphs and sexes (all $\chi^2 > 15$, df $= 3$, all $P < .014$ after Bonferroni

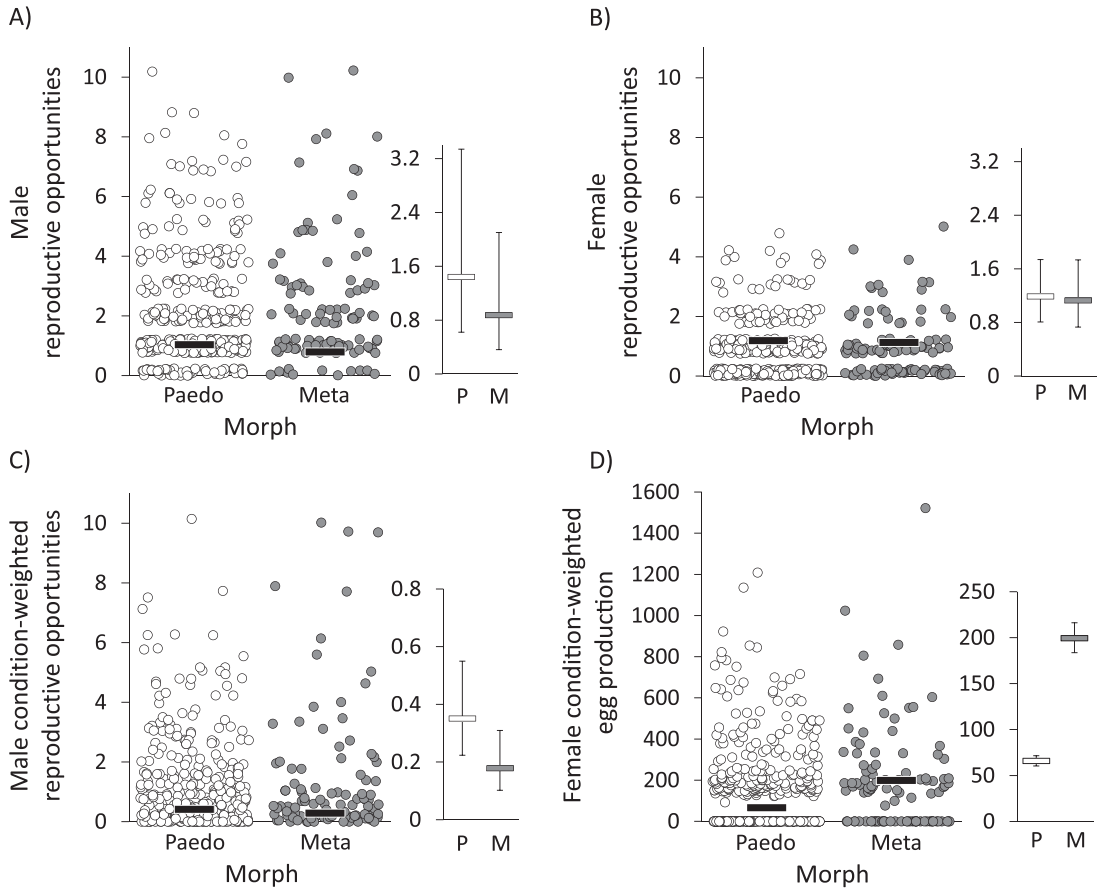

Figure 3: Lifetime fitness metrics for each morph and sex. *A*, Male reproductive opportunities. A reproductive opportunity occurs once per year when an individual is caught in reproductive condition (for details, see "Methods"). *B*, Female reproductive opportunities. *C*, Male condition-weighted reproductive opportunities, where males in higher condition than average males in reproductive condition within a year have a positively weighted number of reproductive opportunities. *D*, Female condition-weighted egg production. Lifetime egg production is the estimated number of eggs per female per lifetime based on her average adult condition in reproductive years and calculated from a population-specific correlation between adult body condition and clutch size. Each circle represents an individual. Circles are jittered along the *Y*-axis ± 0.25 (*A* and *B*) and along the *X*-axis (*A*–*D*) to show the majority of individuals. Bars show means both with and without observations (*inset*). Error bars in the insets are 95% confidence intervals. P = paedomorph; M = metamorph.

adjustments for multiple tests; full results are in table C1), which justified running path analysis separately for each morph and sex.

We next tested the fit of each hypothesized model for each morph and sex. For paedomorphic males, model 2 was the best fit ($\chi^2 = 0.11$, df = 1, $P = .74$). All other models had poor fit ($\chi^2 \geq 10.1$, df = 1 or 2, $P \leq .006$). For paedomorphic females, all three models were a moderately poor fit using the maximum likelihood χ^2 criterion (all $\chi^2 > 5.8$, $P < .015$), but other fit statistics, such as the goodness-of-fit statistic, suggested a good fit for all models (all goodness-of-fit statistics > 0.97, with values closer to one indicating a good fit). For metamorphic males and females, all models tested were a good fit for the data (all $\chi^2 < 3.41$, df = 1 or 2, and $P > .12$). Thus, for consistency, we used model 2 for all morphs and sexes. Full results for model fit statistics are provided in table C2.

For both sexes of each morph, salamanders had more reproductive opportunities when they lived longer and/or began breeding earlier in their lifetime (longevity: $F_{1,269} = 80.31$, $P < .0001$; age at first reproduction: $F_{1,269} = 30.95$, $P < .0001$; figs. 2, 4). Longevity and age at first reproduction were positively correlated; earlier breeders had shorter life spans on average (fig. 2). Paedomorphs bred earlier than metamorphs on average ($F_{1,267} = 6.24$, $P = .0131$), which contributed to a steeper slope for age at first reproduction versus longevity in paedomorphs compared to metamorphs (interaction effect: $F_{1,263} = 7.45$, $P = .0068$; fig. 5). Last, higher adult condition weakly but significantly predicted longer life span ($F_{1,263} = 18.03$, $P < .0001$; fig. 2). Higher adult condition

Table 1: Sex ratios in each morph by cohort and larval pond

Cohort	Larval pond	Sex ratio				Sex ratios differ from 50:50 within morphs?	χ^2	P	Sex ratios differ between morphs?
		Metamorph		Paedomorph					
		Female	Male	Female	Male				
A. Whole population:									
All	All	166 (+)	123 (−)	597 (+)	431 (−)	Female bias in both morphs	.34	.8469	No
B. By cohort:									
1988	All	42	34	163	193	No	2.26	.1331	No
1990	All	16 (+)	5 (−)	13	14	Female bias in metamorphs	3.88	**.0487**	Yes
1998	All	20	12	23	32	No	3.49	.0628	Nearly significant, more female bias in metamorphs vs. more male bias in paedomorphs
1999	All	26	17	36	36	No	1.19	.2760	No
2000	All	25	28	258 (+)	124 (−)	Female bias in paedomorphs	8.49	**.0036**	Yes
2001	All	23	20	93 (+)	26 (−)	Female bias in paedomorphs	9.45	**.0021**	Yes
C. By cohort and pond:									
1988	1	11	12	77 (−)	110 (+)	Male bias in paedomorphs	.37	.5419	No
1988	5	6	6	64	57	No	.04	.8482	No
1988	12	20 (+)	9 (−)	3 (−)	13 (+)	Female bias in metamorphs, male bias in paedomorphs	10.41	**.0013**	Yes
1990	12	12	5	6	6	No	1.27	.2604	No
1998	1	8	2	18	26	No	4.99	**.0255**	Yes, more female bias in metamorphs vs. more male bias in paedomorphs
1999	5	2	6	6	8	No	.70	.4023	No
2000	1	8	2	200 (+)	95 (−)	Female bias in paedomorphs	.66	.4154	No
2000	5	2	6	32	20	No	3.77	.0522	Nearly significant, more male bias in metamorphs vs. more female bias in paedomorphs
2000	12	14	20	3	4	No	.01	.9345	No

Note: Number of females and males from each morph, including breeding and nonbreeding adults. In part A, counts include adults from all cohorts and ponds ($N = 1{,}317$). In part B, we compared sex ratios of each morph in each cohort with at least five female and five male salamanders of each morph captured across all ponds. In part C, we compared sex ratios of each morph with at least six salamanders of each morph (across the sexes) captured in each pond for each cohort. Within morph, we tested whether sex ratios differed from 50:50. When the χ^2 P value was $P < .05$, a plus sign indicates the sex that was more common, and a minus sign indicates the sex that was less common within morph. Between morphs, we tested whether sex ratios differed between metamorphs and paedomorphs, and we report χ^2 values and P values. Statistically significant P values are shown in boldface.

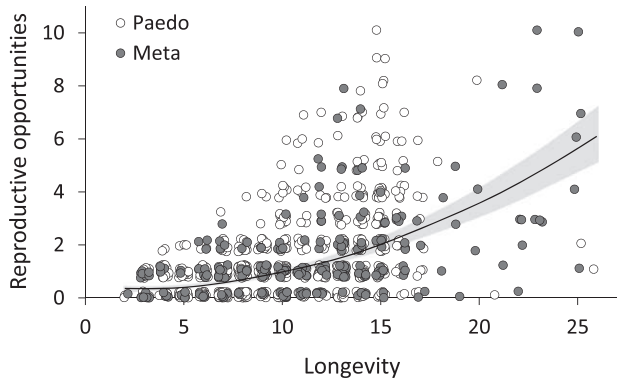

Figure 4: Relationship between longevity and reproductive opportunities. Circles show individuals of each morph in white (paedomorph) or dark gray (metamorph). The solid line shows the predicted relationship between longevity and reproductive opportunities, which did not differ between morphs. The light gray shading shows the 95% confidence interval around the slope. Both reproductive opportunities and longevity are jittered ± 0.25.

also weakly predicted later first breeding events ($F_{1, 267} = 16.90$, $P < .0001$) in all morphs and sexes except metamorphic females (fig. 2).

While relationships among adult life-history traits were similar between morphs and sexes, relationships between larval condition and adult life-history traits differed considerably between the morphs and sexes. Larvae in higher condition that became paedomorphic males or females bred earlier and had higher adult condition. However, in metamorphs, larval condition did not predict age at first reproduction or adult condition (age at first reproduction morph interaction effect: $F_{1, 267} = 17.34$, $P < .0001$; fig. 6*A*, 6*B*; adult condition morph interaction effect: $F_{1, 262} = 25.62$, $P < .0001$; fig. 6*C*, 6*D*; significant slopes for paedomorphs: $t > 5.37$, $P < .0001$; fig. 6*A*, 6*C*; nonsignificant slopes for metamorphs: $t < 0.43$, $P > .66$; fig. 6*B*, 6*D*). Path analysis results were similar; however, instead of no relationship between larval condition and age at first reproduction for metamorphic males, path analysis predicted a weak but significant relationship (path coefficient $= -0.28$, $P = .0045$; fig. 2).

Differences between the sexes in life-history patterns were similar across morphs. For both morphs, males started breeding earlier ($F_{1, 269} = 4.00$, $P = .046$; male: 8.049 [5.959–10.873] years; female: 8.927 [6.511–12.239] years) and had lower adult condition ($F_{1, 268} = 26.64$, $P < .0001$; male: 0.146 [0.107–0.185]; female: 0.179 [0.138–0.220]) on average compared to females. On average, larval condition did not differ between morphs or sexes (fig. D1).

Environmental Effects on Lifetime Fitness and Life History

We tested how environmental variation across space and time affected reproductive opportunities and each life-history trait. We present the terms included in each model and model output in tables A1 and A2, respectively. For our measures of lifetime fitness, we found no effects of larval pond or cohort

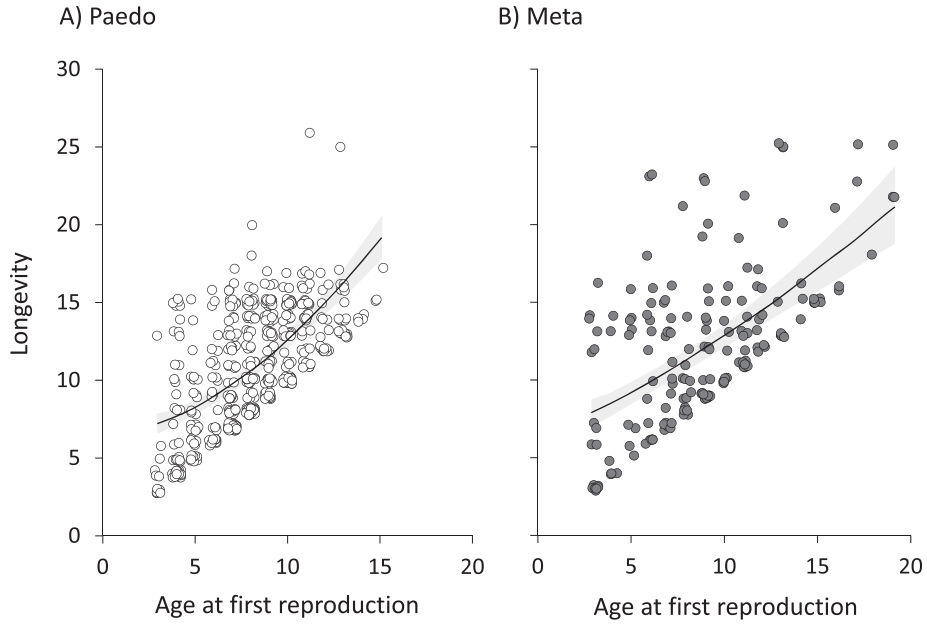

Figure 5: Relationship between age at first reproduction and longevity for paedomorphs (*A*) and metamorphs (*B*). Each circle represents an individual, and circles are jittered ± 0.25 for both longevity and age at first reproduction. Black lines show the predicted slopes, and the light gray shading shows the 95% confidence interval around each slope.

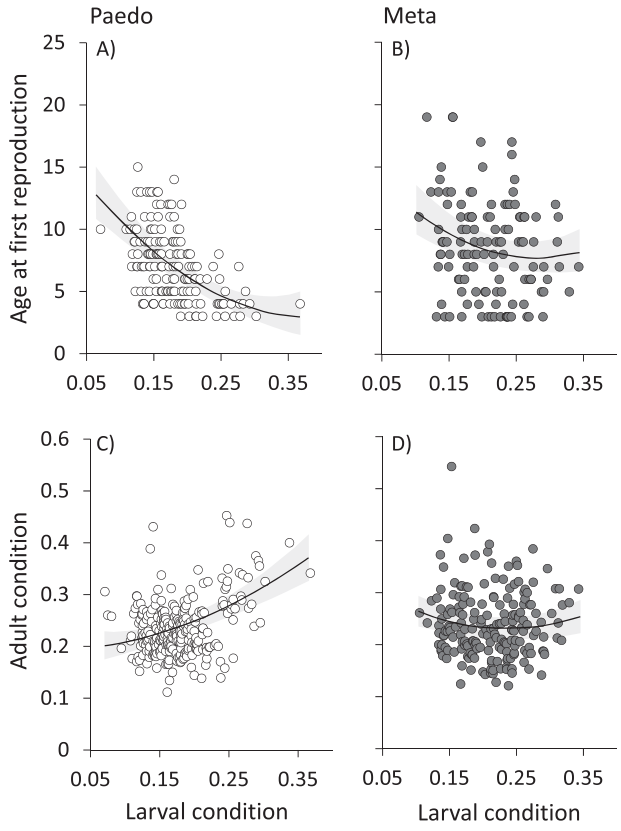

Figure 6: Relationships between larval condition and age at first reproduction for paedomorphs (*A*) and metamorphs (*B*) as well as between larval condition and adult condition for paedomorphs (*C*) and metamorphs (*D*). Circles represent individuals, and the points are not jittered. Black lines show the predicted slopes, and the light gray shading shows the 95% confidence interval around each slope. In *B* and *D*, the slopes for metamorphs are not statistically different from zero.

on number of reproductive opportunities, for the sexes combined or analyzed separately, or for female estimated egg production. For male condition-weighted number of reproductive opportunities, only one of eight cohorts had a significant effect, and we found no effect of larval pond. We also found no effect of larval pond or cohort on longevity. Only one larval pond significantly affected age at first reproduction, and a single cohort significantly affected adult condition. While the effects of environmental variation were limited on adult life history and fitness, larval pond and cohort explained relatively more variation in larval condition, with significant effects of three ponds and one cohort.

Discussion

From a 27-year data set encompassing eight generations of salamanders, we found that average lifetime fitness differed between morphs with sex-specific fitness advantages for paedomorphic males and metamorphic females. Morphs also differed in life-history strategies that affected fitness with earlier first breeding events in paedomorphs and longer life spans in metamorphs. Last, spatiotemporal variation contributed to variation in life history and fitness within morphs more than between morphs.

Estimates of lifetime fitness revealed differences in relative fitness of each sex between morphs. Paedomorphic males had more reproductive opportunities than metamorphic males when accounting for potentially higher mating success of larger males. In contrast, metamorphic females had higher estimates of lifetime egg production than paedomorphic females. Our findings are consistent with the general pattern that selection to maximize reproductive success favors more matings in males and higher fecundity in females (Bateman 1948; Andersson 1994). Because we statistically controlled for life-history traits in our analysis, these results reveal that morph and sex differences in fitness extend beyond life-history differences. These sex-specific lifetime fitness advantages that differ between morphs could contribute to maintaining the polyphenism in this population.

If paedomorphic males and metamorphic females were consistently favored over the alternative morph-sex combinations, this could generate strong, sexually antagonistic selection and potentially favor sex-limited morph expression (Rice 1984; Wedell et al. 2006; Bonduriansky et al. 2008). We would then expect sex ratios to differ between the morphs with high relative frequencies of males in paedomorphs and females in metamorphs (e.g., Mathiron et al. 2017). Previous work analyzing a subset of the data we used here (4 years of observations vs. 27 years in the current study) detected sex ratio differences between morphs consistent with these predictions (Whiteman 1997). In this study, we found that sex ratio differences between morphs varied across cohorts and larval ponds. Between 1988 and 1999, some cohorts and larval ponds produced sex ratios consistent with our findings of sex-specific fitness differences between morphs (i.e., more metamorphic females and paedomorphic males). Later cohorts, 2000 and 2001, tended to produce sex ratios in the opposite direction (i.e., biased toward paedomorphic females). Also, some cohorts and larval ponds showed no differences in sex ratio between morphs.

There are multiple reasons why the extent or direction of sex ratio differences between morphs may vary across time and space. Sex ratios that differ from 50 : 50 expectations could result from differential survival to adulthood of each sex within a morph and/or sex-biased morph production. First, survival to adulthood depends on competition and resource quality that varies across cohorts and ponds as well as yearly variation in abiotic factors, including temperature, dissolved oxygen concentration, and snowpack (Whiteman et al. 1994, 2012; Wissinger et al. 2003; Whiteman and Wissinger 2005). Second, selection for sex-biased morph production is likely

shaped by multiple sources and constraints. Sex-specific differences in lifetime fitness between morphs likely generated consistent selection for sex-biased morph production because we found that lifetime fitness did not vary across cohorts or larval ponds. However, selection on morph production may be stronger at the larval stage than at the adult stage. Larval condition strongly influences morph production (Whiteman 1994; Whiteman et al. 2012). On average, larval condition did not differ between the sexes of each morph (this study), which suggests that selection could act similarly across the sexes for morph production. Yet differences in minimum larval condition for each sex of each morph (fig. D1) suggest that reaction norms for morph production may differ between the sexes. Indeed, selection could act on a component of reaction norms (e.g., environmental sensitivity) differently in each sex (Schlichting and Pigliucci 1998). Environmental variation could then shift morph production within the sexes across time and space. Sex-biased morph production could also be constrained by a shared genetic basis for morph development between the sexes (e.g., Roff and Fairbairn 1993). If selection on developmental traits acts in opposite directions in each sex, this could result in intralocus sexual conflict (Bonduriansky and Chenoweth 2009; Cox and Calsbeek 2009; Poissant et al. 2010). Additionally, interbreeding between morphs is common (this population [Whiteman et al. 1999; H. H. Whiteman, unpublished data]; polyphenic newts [Oromi et al. 2016]), which may further limit the evolution of sex ratio differences between morphs.

For adaptive polymorphisms across multiple taxa, differences in life-history strategies between morphs are common because morphs experience different selective regimes that can affect growth rate, timing and extent of reproduction, and life span (Day et al. 1994; Skúlason and Smith 1995; Jonsson and Jonsson 2001; Nijhout 2003; Moczek et al. 2011; Moyers and Rieseberg 2016). In our study, paedomorphs and metamorphs used different life-history strategies that maximize alternative ends of the trade-off between age at first reproduction and longevity. In both morphs, longer life span and earlier age at first reproduction predicted more reproductive opportunities. Yet physiological trade-offs between energy allocated to survival and reproduction limit individuals from being able to maximize both fitness components (Roff 1992; Stearns 1992), and such trade-offs are common between alternative, plastic phenotypes (Roff 1996). On average, paedomorphs bred earlier and died earlier compared to metamorphs. Forgoing metamorphosis may allow paedomorphs to allocate energy to growth and reproductive development sooner than metamorphs (Ryan and Semlitsch 1998). Similarly, in multiple insect species with developmental wing polymorphisms, the wingless morph that invests less energy in development breeds earlier on average (Denno et al. 1989; Roff and Fairbairn 1991; Ishikawa and Miura 2009). In contrast to the early breeding strategy in paedomorphs, delaying age of first reproduction may allow metamorphic females to gain a reproductive advantage over paedomorphic females by investing more energy in adult body condition, which correlates with greater egg production (Stearns 1992; this study).

In addition to life-history differences between morphs, life-history trait values varied within morphs, which suggests plasticity of life-history traits within morphs (Nijhout 2003). The distributions of longevity and age at first reproduction for each morph overlapped considerably. In fact, some metamorphs bred as early in their lifetimes as paedomorphs, so metamorphosis did not physiologically constrain early breeding for all metamorphs. While earlier breeding in metamorphs was not strongly predicted by higher body condition for larvae or adults, earlier breeders often had shorter life spans. The extent to which individuals experience costs and trade-offs associated with certain life-history strategies likely depends on many factors, including age, previous reproductive effort, and resource availability (Blanckenhorn 1998; Zhang and Hood 2016; Panagakis et al. 2017). Moreover, the mean differences between morphs in longevity and age at first reproduction are likely driven by a subset of metamorphs that had later first breeding events and longer life spans. By breeding later and living longer, these metamorphs could achieve equal reproductive success compared to paedomorphs that bred and died earlier. Long-lived metamorphs may offset costs of breeding by increasing years between breeding events, like in many iteroparous organisms (Boekelheide and Ainley 1989; Roff 1992; Stearns 1992; Church et al. 2007). Indeed, across multiple taxa, fewer reproductive events often correlated with a longer life span (Roff 1992; Stearns 1992).

While the presence and direction of relationships among adult life-history traits were similar between morphs, the relationships between larval condition and adult life-history traits differed strikingly between morphs. Higher larval condition predicted earlier breeding, higher adult condition, and shorter life span for paedomorphs; however, for metamorphs, higher larval condition only weakly predicted earlier breeding and did not affect adult condition or longevity directly. Larval condition likely predicted adult condition in paedomorphs but not metamorphs for multiple, non–mutually exclusive reasons. First, paedomorphs retain their larval characteristics and avoid energetic costs of metamorphosis (Wilbur 1980; Whiteman 1994); thus, larval and adult condition should be more similar in paedomorphs than in metamorphs. Studies of amphibians, insects, and marine invertebrates that undergo metamorphosis find mixed evidence of carryover effects from larval to adult traits (Semlitsch et al. 1988; Scott 1994; De Block and Stoks 2005; Crean et al. 2011; Schmidt et al. 2012; Earl and Semlitsch 2013; Green and Bailey 2015; Müller et al. 2016). Hence, metamorphosis does not necessarily erase effects of the larval environment. In our study system, metamorphs have a longer growth period between the larval stage and reproductive maturity than paedomorphs (i.e., later age

at first reproduction in metamorphs). A longer time lag between larval and adult life stages predicts a weaker relationship between larval and adult traits (Earl and Whiteman 2015). Last, paedomorphs stay in their natal ponds and so experience a similar environment as larvae, whereas metamorphs disperse into the terrestrial environment (Wilbur 1980; Whiteman et al. 1994). Variation in the terrestrial environment might overwhelm variation from the aquatic, larval environment and minimize the effects of larval environments on metamorphic adult traits (Earl and Semlitsch 2013).

Spatiotemporal variation significantly affected life-history traits of both morphs, with most effects on larval condition. This fits with previous work in this system that competitor density and relative growth rate vary across ponds and cohorts and primarily determine morph production (Whiteman et al. 2012). Spatiotemporal variation minimally affected lifetime reproductive opportunities. Instead, variation in life-history traits, especially age at first reproduction and longevity, explained most of the variation in reproductive opportunities within and between morphs. Overall, spatiotemporal variation contributed more to variation in life-history traits early versus later in life. Thus, spatiotemporal variation likely plays a larger role in morph production (Whiteman and Wissinger 2005; Whiteman et al. 2012) than morph maintenance.

The factors that favor the initial evolution of a polyphenism may differ from those that maintain it. The evolution of polyphenism requires both environmental variation that alters selection across time or space and cues that allow organisms to predict environmental conditions (Levins 1968; West-Eberhard 1989, 2003; Wilson 1989; Moran 1992; Skúlason and Smith 1995; Gross 1996; Roff 1996; Sultan and Spencer 2002). Plasticity of morph production should be maintained when an environmentally sensitive phenotype has higher fitness than a constitutively expressed phenotype (e.g., for seasonal morphs or environments that change irregularly; Skúlason and Smith 1995; Simpson et al. 2011). Negative frequency- or density-dependent selection can maintain a polyphenism when competition occurs more often within morphs than between morphs (West-Eberhard 1989; Wilson 1989; Pfennig 1992; Simpson et al. 2011). Plasticity is likely maintained when a trait is highly plastic, which allows the population to get closer to an adaptive peak without genetic change and thus weakens selection for the genetic component underlying the trait (Pfennig et al. 2010). In this study, we found sex-specific advantages that differed between morphs. The morphs and sexes maximized lifetime reproductive success via different life-history strategies, especially by maximizing opposite ends of the trade-off between age at first reproduction and longevity. Last, spatiotemporal variation shaped variation in early life-history traits but may contribute little to maintaining this polyphenism.

To understand how a polyphenism is maintained, it is critical to measure the fitness of each morph and sex across time and space. While multiple studies have estimated fitness components of alternative morphs (e.g., Lively 1986; Pfennig 1992; Roff 1996; Moczek 1998), we provide unique insight into the adaptive significance of a developmental polyphenism by measuring lifetime fitness in a long-term study that monitored eight generations of tiger salamanders for 27 years. Our findings suggest that sex differences in fitness within morphs could contribute to the maintenance of polyphenism. Building on theory that predicts when polyphenism is likely to occur in environments that vary either temporally or spatially (Moran 1992; Tufto 2000; Sultan and Spencer 2002) and the extensive body of literature examining sex differences in selection (e.g., Lande 1980; Rice 1984; Preziosi and Fairbairn 2000; Arnqvist and Rowe 2005; Bonduriansky and Chenoweth 2009; Cox and Calsbeek 2009; Mathiron et al. 2017; Connallon et al. 2018, 2019; Hämäläinen et al. 2018), future work is needed to test how morph-specific sex differences in fitness, genetic correlations between sexes for morph production, life-history differences between morphs and sexes, and environmental variation across time and space can maintain a polyphenism.

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