Frequency-Dependent and Correlational Selection Pressures Have Conflicting Consequences for Assortative Mating in a Color-Polymorphic Lizard, *Uta stansburiana*

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ABSTRACT: Genetically determined polymorphisms incorporating multiple traits can persist in nature under chronic, fluctuating, and sometimes conflicting selection pressures. Balancing selection among morphs preserves equilibrium frequencies, while correlational selection maintains favorable trait combinations within each morph. Under negative frequency-dependent selection, females should mate (often disassortatively) with rare male morphotypes to produce conditionally fit offspring. Conversely, under correlational selection, females should mate assortatively to preserve coadapted gene complexes and avoid ontogenetic conflict. Using controlled breeding designs, we evaluated consequences of assortative mating patterns in color-polymorphic side-blotched lizards (*Uta stansburiana*), to identify conflict between these sources of selection. Females who mated disassortatively, and to conditionally high-quality males in the context of frequency-dependent selection, experienced highest fertility rates. In contrast, assortatively mated females experienced higher fetal viability rates. The trade-off between fertility and egg viability resulted in no overall fitness benefit to either assortative or disassortative mating patterns. These results suggest that ongoing conflict between correlational and frequency dependent selection in polymorphic populations may generate a trade-off between rare-morph advantage and phenotypic integration and between assortative and disassortative mating decisions. More generally, interactions among multiple sources of diversity-promoting selection can alter adaptations and dynamics predicted to arise under any of these regimes alone.

Keywords: fitness epistasis, prezygotic isolation, postzygotic incompatibility, sympatric speciation, fluctuating selection, cryptic female choice.

Introduction

Many species demonstrate conspicuous polymorphisms in which morphs are genetically distinct, incorporate mul-

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tiple, often unlinked traits, and persist over long timescales while remaining interfertile with each other (Ford 1945). The existence of such complex polymorphisms is a remarkable phenomenon, because their maintenance within a population involves the chronic action of multiple and sometimes conflicting sources of selection.

In order to stably persist, genetically determined alternative morphotypes must have equal average fitness over time (Slatkin 1978; Maynard Smith 1982), and these may be maintained by a variety of intrinsic or extrinsic mechanisms. One common mechanism maintaining alternative morphotypes is balancing selection, including negative frequency-dependent selection, under which rare phenotypes experience a mating or survival advantage over more common morphs (Partridge 1988; Olendorf et al. 2006). Negative frequency-dependent selection resulting in stable polymorphisms can be driven by predator switching behavior (favoring rare antipredator strategies; Punzalan et al. 2005), competition for mates or resources (favoring rare mating or resource acquisition strategies; Gross 1991; Smith and Skulason 1996), or parasitism (favoring rare host genotypes or immune strategies; Dybdahl and Lively 1998).

Under chronic and predictable patterns of negative frequency-dependent selection driven by one of the mechanisms described above, females (or the non-mate-limited sex) should benefit by mating with males that are predicted to sire rare morphotypes, in order to produce offspring that have high fitness due to their paternally inherited, rare attributes (Alonzo and Sinervo 2001; Qvarnström 2001; Welch 2003; Royle et al. 2008). Preference for rare males leads to largely disassortative mating patterns, because most choosing females will exhibit common morphotypes. The evolution of preferences for rare morphotypes in the context of a preexisting negative frequency-dependent selection regime can further contribute to the rare-morph advantage.

These preferences can then help stabilize the polymorphism by facilitating faster returns to equilibrium morph frequencies after perturbation (Alonzo and Sinervo 2001; Rolan-Alvarez et al. 2012).

When multiple, morph-specific traits are each determined by different underlying genes, morphs can be said to represent alternatively coadapted gene complexes (Sinervo and Svensson 2002; Bleay and Sinervo 2007). In addition to physical linkage or pleiotropy, alternative patterns of genetic integration within each morph can be maintained over the long term by chronic correlational selection, or multivariate selection favoring specific combinations of traits (Roff and Fairbairn 2012). For example, individuals expressing alternative color patterns are also commonly selected to express alternative behaviors, with different behaviors specifically favored in combination with each color pattern (Brodie 1992; Forsman and Appelqvist 1998). While correlational selection contributes to the preservation of alternatively adapted types in the population, interbreeding between morphs breaks apart favorable trait combinations, and offspring of intermorph matings may experience decreased fitness under correlational selection (Brodie 1992). Correlational selection can, therefore, impose a weak postzygotic barrier to reproduction between alternative morphs (Pryke and Griffith 2009; Corbett-Detig et al. 2013). Assortative mating with respect to morphotype prevents the erosion of coadapted gene complexes and is thus predicted to be favored under chronic correlational selection regimes (Lande 1984; Sinervo and Svensson 2002; Bleay and Sinervo 2007; Caesar et al. 2007; ten Tusscher and Hogeweg 2009; Pérez i de Lanuza et al. 2013).

Both the genetic conflict among morphs generated by correlational selection itself and assortative mating arising under correlational selection can introduce genetic divergence among morphs (ten Tusscher and Hogeweg 2009; Huyghe et al. 2010). Genetic divergence further reduces the fitness of intermorph hybrids by introducing additional sources of postzygotic incompatibility (e.g., a form of outbreeding depression leading to poor physiological performance or to embryonic malfunction; Linn et al. 2004; Pryke and Griffith 2009). Assortative mating preferences arising under correlational selection can also introduce a source of positive frequency-dependent selection on common morphs. Positive frequency-dependent selection arises under assortative mating because common morphs of the mate-limited sex (usually males) experience the greatest number of mating opportunities when females prefer to mate assortatively (Kirkpatrick and Nuismer 2004). Under some conditions, genetic incompatibilities and positive frequency-dependent selection arising from correlational selection and assortative mating are predicted to lead to the loss of morphs (Kirkpatrick and Nuismer

2004). Loss of morphs could, in turn, reduce the population's niche breadth (Forsman and Aberg 2008) or possibly contribute to socially mediated speciation if allopatric populations fix for different morphotypes (West-Eberhard 1986; Corl et al. 2010; Hugall and Stuart-Fox 2012). Whether polymorphic populations can remain stable over long time periods may depend critically on the relative strengths of correlational selection, which tends to destabilize polymorphism through assortative mating, and negative frequency dependent selection, which promotes disassortative mating patterns that help preserve the polymorphism. Understanding the net fitness consequences accruing from assortative versus disassortative matings in a polymorphic population might, therefore, provide important insights into the balance between negative frequency-dependent selection and correlational selection.

We tested the relative benefits to females of assortative and disassortative mating in the context of a long-studied population of side-blotched lizards (*Uta stansburiana*), in which alternative throat colors signal discrete reproductive strategies (i.e., morphotypes, or morphs) within each sex that each have a competitive advantage when rare. Morphs of this species involve multiple complex traits, and we have previously reported strong correlational selection favoring and preserving alternative combinations of behavior, reproductive physiology, immune function, stress response, and antipredator strategies within each morph (Sinervo et al. 2000a, 2006b; Sinervo and Svensson 2002; Lancaster et al. 2007, 2009, 2010; Mills et al. 2008; Svensson et al. 2009). In addition, females have been shown to exhibit partially assortative behavioral mating preferences, which act to limit the erosion of coadapted gene complexes (Bleay and Sinervo 2007). Conversely, game-theoretical modeling has predicted that female *U. stansburiana* should maximize their fitness by mating (disassortatively) with rare morphotypes, in order to produce sons with a frequency-dependent advantage in intrasexual competition for mates (Alonzo and Sinervo 2001).

Material and Methods

Study System

Our long-term study population of *Uta stansburiana* at Los Baños Grandes, Merced County, California, exhibits three alternative throat colors of orange (O), blue (B), and yellow (Y). Linkage mapping (Sinervo et al. 2006b), laboratory crosses (Sinervo 2001), and a field pedigree (Sinervo 2001; Sinervo and Zamudio 2001) indicate that throat color is coded by three alleles (*o*, *b*, *y*) at a single locus (OBY). Homozygotes exhibit pure throat colors, while *bo* and *by* heterozygotes exhibit discrete patches of both blue

and orange or yellow coloration, and *yo* heterozygotes exhibit a dull, peach-colored throat. Therefore, genotypes of adult lizards can be estimated by sight. However, while the *oby* alleles are codominant with respect to color expression, they exhibit dominance with respect to underlying strategy type ($o > y > b$; Sinervo and Zamudio 2001). In males, alternative throat colors signal alternative mating strategies: O males ($= oo$, *bo*, and *yo* genotypes) are usurpers, Y males ($= by$ and *yy* genotypes) are sneakers, and B males ($= bb$ genotype) are mate guarders. Males compete for access to females, and these alternative strategies each have an advantage in direct competition for mates when rare, such that male fitness with respect to morph is negatively frequency dependent and morph frequencies stably cycle in the population over 4–5 years in a "rock-paper-scissors" game (Sinervo and Lively 1996). In females, throat color signals reproductive strategies, with O females laying large clutches of small eggs while Y and B females lay small clutches of large eggs (Sinervo et al. 2000*b*). Alternative female morphs are maintained by density-dependent selection: O females have higher fitness at low density, while Y and B females have higher fitness at high density (Sinervo et al. 2000*b*). Because of strong competition for mates among males, females are not mate or sperm limited and usually mate multiply in the wild (Zamudio and Sinervo 2000). Lizards reach reproductive maturity and reproduce within 1 year and rarely live longer than a single breeding season; generations are therefore largely nonoverlapping.

Alternative, coadapted gene complexes in this species may partially reflect a physical linkage group containing genes for many morph-specific traits as has been documented in other species (Takahashi et al. 2012). However, previous correlational selection studies (cited above) indicate that many other traits involved in morph complexes are likely not physically linked to throat color (Sinervo et al. 2006*b*; Lancaster et al. 2007).

Breeding Experiment

In 2004 and 2006, we conducted lab crosses of *U. stansburiana* collected at our primary study population, with breeding and housing methods as described by Lancaster et al. (2007, 2010). Lizards were captured from the wild in early spring, just before reaching reproductive maturity. Each female considered in our analysis was paired with a single, unique male in an individual breeding enclosure ($n = 81$ of such breeding units in 2004 and $n = 56$ in 2006, for a total of $n = 137$ breeding units over both years). Breeding units originally consisted of 2–3 females per male, but only 1 female per male was randomly selected for this study. Females laid 1–4 clutches each, over the course of the season. Four of our breeding units in 2004 did not result in any clutches produced, and are

eliminated from the analysis, resulting in a total $n = 133$ mated females analyzed for mating outcomes and fitness.

Freshly laid eggs were visually scored as fertilized (plump, ivory-colored, and with a visible, pink embryo spot) or unfertilized (yellow and rubbery, no visible embryo). As part of a separate experiment, two fertile eggs from each clutch were randomly selected for yolk sampling, in which 20% of the yolk was removed by aspirating with a syringe. Although this procedure slightly increases egg mortality (Sinervo and Huey 1990), we included these "miniaturized" eggs in our analysis because the procedure was uniformly applied across all clutches. Fertile eggs were incubated as previously described (Lancaster et al. 2007), and marked hatchlings were returned to the field site at randomized locations within 3 days of birth. We returned to the field site to monitor released progeny for survival to adulthood the following spring, using census methods described in Sinervo et al. (2006*a*). Data for this study are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.g924s (Lancaster et al. 2014).

Statistical Analysis

Mating Outcomes

We tested for effects of assortative versus disassortative mating on fertility, egg viability, and offspring survival in JMP v9.0.2 (SAS Institute, Cary, NC), using generalized linear models (GLMs) with a binomial error distribution and logit link function. To estimate effects on fertility, we used as our response variable $k =$ the total number of fertilized eggs laid by a female over the reproductive season, out of $n =$ the total number of eggs laid by the female, including all unfertilized eggs. To estimate effects on egg viability, we used as our response variable $k =$ total number of live progeny produced by each mated pair, out of $n =$ total number of fertile eggs laid by the female. To estimate effects on offspring survival, we used as our response variable $k =$ total number of progeny surviving to adulthood, out of $n =$ total number of hatched progeny from each breeding pair. Reported error terms are standard errors.

In each of the tests for fertility and postzygotic viability, we examined whether these mating outcomes were affected by assortative mating for throat color and by the dynamics of negative frequency-dependent selection. We scored matings as being assortative by throat color morphotype (e.g., an O female mated to an O male) or disassortative (e.g., an O female mated to a B male). In the same model, we also tested whether mating outcomes were adaptive in the context of the negative frequency-dependent, rock-paper-scissors male fitness cycle (Sinervo and Lively 1996), that is, whether mating outcomes were more favorable when

females were mated to conditionally high-quality males, which were those most likely to produce high-fitness son morphotypes in the next generation. We estimated the conditional quality of males in our crosses as the predicted (frequency-dependent) siring success of sons who inherit his (their sire's) morphotype, using a previously constructed matrix of conditional siring probabilities (C. Bleay and B. Sinervo, unpublished data; table 1) and male morph frequencies in the year in which progeny matured (2005 and 2007). For example, long-term field observations and paternity data (C. Bleay and B. Sinervo, unpublished data) indicate that O males have a probability of siring success when in competition with other O males of $P(O \mid O) = 0.22$, a probability of siring success in competition with Y males of $P(O \mid Y) = 0.16$, and a probability of siring success in competition with B males of $P(O \mid B) = 0.57$ (table 1). In 2005, morph frequencies were as follows: $f_O = 0.02$, $f_Y = 0.45$, and $f_B = 0.53$. Therefore, the predicted fitness of O sons (maturing in 2005) from pairs mated in 2004 was $w_O = P(O \mid O) \times f_O(t) + P(O \mid Y) \times f_Y(t) + P(O \mid B) \times f_B(t) = 0.22 \times 0.02 + 0.16 \times 0.45 + 0.57 \times 0.53 = 0.38$. Additional calculations are presented in table 1. To control for idiosyncratic effects due to the specific phases of the morph frequency cycle present in the 2 years of our study, we included the relative morph frequencies of sires as a covariate in analyses that included conditional male quality as an explanatory variable. Sire morph frequencies cycle around different means, so the frequency of each sire's morph in the wild during the year of the experiment (2004 or 2006) was divided by its long-term

average frequency (over the period of 1990–2007) to obtain a covariate for relative sire morph frequency and current cycle phase.

Fitness Consequences

Assortative and disassortative matings have different predicted benefits and costs. We ran a combined analysis of costs and benefits to females from assortative versus disassortative matings within each year of our study and across years. For females mated assortatively (O × O, Y × Y, and B × B) versus disassortatively (O × Y/B, Y × O/B, and B × O/Y), we calculated the average rates of fertility (fertilized eggs/total eggs), fertile egg survivorship (hatchlings/fertilized eggs), and the predicted siring success of sons (as described below). For the fertility and egg survivorship fitness components, means, standard errors, and significance were calculated using a binomial GLM, while mean fitnesses from expected son siring success were estimated and compared using standard least squares.

The female fitness component resulting from the expected siring success of her sons in the context of the rock-paper-scissors male fitness cycle was estimated for each mated pair as the probability of producing sons of each male morph (juveniles do not exhibit throat coloration, so offspring throat color probabilities were constructed based on maternal and paternal genotypes), multiplied by the predicted fitness of each morph in the following year in the context of the rock-paper-scissors cycle (predicted fitness calculated as described above and in table 1),

Table 1: Predicted fitness of sons in the year(s) following the breeding study

Matrix of conditional mating probabilities, in competition with each morphotype:			Probability of competition against each morphotype:		Vector of predicted fitness (unstandardized):	
	Orange	Yellow	Blue		2005 morph frequencies		Sons' fitnesses in 2005
Orange	.22	.16	.57	$f_O(t) =$	.02	$w_O = P(O \mid O) \times f_O(t) + P(O \mid Y) \times f_Y(t) + P(O \mid B) \times f_B(t) =$	.38
Yellow	.57	.26	.17	$f_Y(t) =$	.45	$w_Y = P(Y \mid O) \times f_O(t) + P(Y \mid Y) \times f_Y(t) + P(Y \mid B) \times f_B(t) =$	.22
Blue	.20	.58	.26	$f_B(t) =$	.53	$w_B = P(B \mid O) \times f_O(t) + P(B \mid Y) \times f_Y(t) + P(B \mid B) \times f_B(t) =$	.40
					2007 morph frequencies		Sons' fitnesses in 2007
Orange	.22	.16	.57	$f_O(t) =$	.35	$w_O = P(O \mid O) \times f_O(t) + P(O \mid Y) \times f_Y(t) + P(O \mid B) \times f_B(t) =$	.22
Yellow	.57	.26	.17	$f_Y(t) =$	.57	$w_Y = P(Y \mid O) \times f_O(t) + P(Y \mid Y) \times f_Y(t) + P(Y \mid B) \times f_B(t) =$	.36
Blue	.20	.58	.26	$f_B(t) =$	.08	$w_B = P(B \mid O) \times f_O(t) + P(B \mid Y) \times f_Y(t) + P(B \mid B) \times f_B(t) =$	.42

Note: Column player in the payoff matrix is the population; row player represents sons.

summed over all possible son morphs. For example, following Mendelian inheritance, a *yo* female and a *bo* male will produce O sons (*yo*, *bo*, and *oo*) with a probability of $P_o = 0.75$, and will produce Y sons (*by*) with a probability of $P_Y = 0.25$. In 2004, the expected contribution of sons' mating success to female fitness within this particular pair would therefore be $P_o \times w_o + P_Y \times w_Y = 0.75 \times 0.38 + 0.25 \times 0.22 = 0.34$. This method of calculating sons' predicted siring success is based on the known dynamics of frequency-dependent selection in this system, which is thought to be the primary driver of male reproductive success (Sinervo and Lively 1996). However, this method does not incorporate any additional, unknown but potentially positive effects of assortative mating on sons' siring success and may therefore bias our combined female fitness estimates toward benefits of disassortative mating.

These three fitness components (fertility, egg viability, and expected siring success of sons) were then multiplied to determine overall female fitness and the direction of selection on female mating patterns within each year. We purposely omitted several components of fitness from our model: we excluded offspring posthatching survivorship, because we did not detect any direct or indirect effects of assortative mating on this fitness component. We also excluded fitness consequences from total number of eggs laid and from daughters' reproductive success, because these values are under density-dependent rather than frequency-dependent selection in this study system (Sinervo et al. 2000*b*). Both 2004 and 2006 were "boom" years of the density cycle, in which female preferences for males that produce conditionally high-fitness sons is predicted to produce larger benefits than preferences based on daughter quality, and the trade-off between conditional quality of sons and daughters is relaxed (Alonzo and Sinervo 2001). We also note that the practice of assigning offspring fitness to parents is controversial and can lead to erroneous conclusions when using such fitness measures to predict evolutionary responses to selection (Wolf and Wade 2001). However, the fitness benefits of reproductive decisions by parents are often accrued through increased offspring survival or reproduction (Fisher 1930; Trivers and Willard 1973), so we have included expected offspring mating success as a component of parental fitness here.

Results

Fertility

Females had higher fertility rates when mated disassortatively than when mated assortatively (effect of disassortative mating on fertility = 0.28 ± 0.09, $\chi^2 = 10.08$, $P = .002$; fig. 1*A*, table 2). Fertility rates were also higher when females were mated to conditionally high-quality

sires, which were defined as those that were more likely to produce high-fitness sons in the context of the rock-paper-scissors frequency-dependent fitness cycle (effect of conditional male quality on fertility = 2.91 ± 1.17, $\chi^2 = 6.59$, $P = .01$; fig. 1*B*).

Fetal and Offspring Viability

Females experienced significantly higher fertile egg viability (i.e., improved hatching rates of fertilized eggs) when mated assortatively with respect to throat color morphotype than when mated disassortatively (effect of assortative mating = 0.16 ± 0.07, $\chi^2 = 5.32$, $P = .02$; fig. 1*C*; table 2). Experimental egg miniaturization, which was uniformly applied to approximately one-third of the eggs from each clutch, did not influence this result. Omitting miniaturized eggs and progeny from the analysis results in the same effect size but slightly higher uncertainty due to reduced data (effect of assortative mating on egg viability, omitting miniaturized eggs and progeny = 0.16 ± 0.09, $\chi^2 = 3.34$, $P = .06$). Egg viability was not affected by whether a female's partner was predicted to sire conditionally high-fitness sons, and this effect was removed from the final model. Posthatching offspring survival rates were not affected by the type of mating (assortative vs. disassortative; $P = .29$) or by the conditional quality of the sire ($P = .17$).

Fitness Consequences

Within each year and across years, we found that disassortative matings resulted in higher female fitness from fertility than assortative matings, while assortative matings resulted in significantly higher female fitness via fertile egg viability rates across years (table 2). The pattern of higher female fitness from fertile egg viability in assortative matings was also evident within each year but was significant only in 2006. Consistent with the observed trade-off conferring higher fertilization rates when females mated disassortatively and with conditionally high-quality sires but higher fertile egg viability rates when females mated assortatively, we found that there was no net fitness benefit to mating assortatively vs. disassortatively in either year of our experiment (table 2).

Sons of rare males are always expected to have higher fitness than sons of common morphotypes in our system. However, contrary to theoretical expectations, we found that the years differed in whether assortative or disassortative mating patterns resulted in females pairing with rare male types. In 2004, we observed the pattern expected under standard frequency-dependent dynamics and observed in our fertility data, in which females mated primarily disassortatively to produce high-fitness son mor-
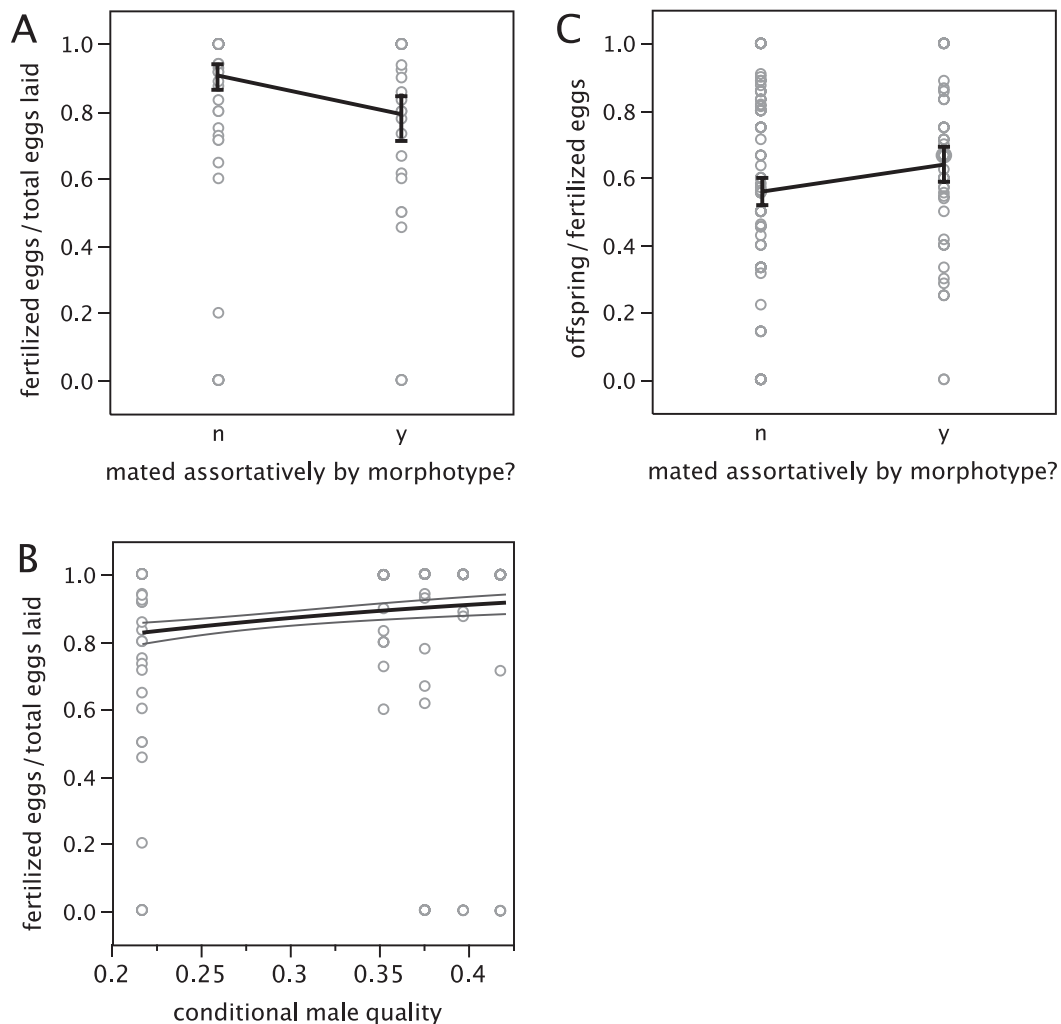
Figure 1: Effects of mating patterns on infertility and egg death. *A*, Females mated disassortatively by throat color morphotype experienced higher rates of fertilization than females mated assortatively. *B*, Females also experienced higher fertilization rates when mated to conditionally high-quality males. Conditionally high-quality males were defined as those with throat color morphotypes that were predicted to confer high fitness to sons in the next generation of the "rock-paper-scissors" male fitness cycle. *C*, Females who mated assortatively experienced higher egg viability rates than females mated disassortatively. Females therefore face a trade-off between fertility (*A*) and egg viability (*C*) when mating either assortatively or disassortatively.

photypes (Alonzo and Sinervo 2001). In 2006, we observed the reverse pattern, and females mated assortatively were more likely to produce sons with predicted high-fitness morphotypes (table 2).

Discussion

We found evidence of a trade-off between assortative and disassortative mating patterns in their effects on fertility and egg viability, with each of these mating patterns benefitting a different component of female fitness (table 2). Fertilization rates were higher when females were mated

disassortatively and when mated to males that were predicted to sire conditionally high-fitness son morphotypes in the rock-paper-scissors cycle of male intersexual competition for mates (fig. 1*A*, 1*B*). In contrast, fertile egg viability was higher when females were mated assortatively than when they were mated disassortatively (fig. 1*C*). These conflicting reproductive outcomes resulted in no net benefit to females of either mating type. The underlying mechanisms contributing to differential fertility and egg viability are unknown, but specific, hypothesized factors leading to the observed trade-off between mating patterns are described below.

Table 2: Female fitness consequences under different mating combinations

Year, mating type	N matings	Fertilized eggs/ total eggs	Hatchlings/ fertilized eggs	Son fitness	Total female fitness	Relative fitness within each year
2004:						
Assortative	26	.77 ± .05*	.66 ± .06	.29 ± .01*	.15 ± .02	.83
Disassortative	51	.84 ± .03*	.64 ± .05	.33 ± .01*	.18 ± .02	1.00
2006:						
Assortative	21	.84 ± .06*	.60 ± .09**	.34 ± .01*	.17 ± .03	1.00
Disassortative	35	.91 ± .04*	.42 ± .06**	.30 ± .01*	.11 ± .02	.67
Combined years:						
Assortative	47	.79 ± .04*	.64 ± .06*	.32 ± .01	.16 ± .02	
Disassortative	86	.87 ± .03*	.56 ± .04*	.31 ± .01	.15 ± .01	

Note: Asterisks indicate where fitness consequences of assortative mating were significantly different from consequences of disassortative mating, within each year and across combined years.

* $P < .05$.

** $P < .01$.

Fertility Effects

Higher fertility under disassortative mating (fig. 1A) for rare or conditionally high-quality sires (fig. 1B) may represent a conditional cryptic female choice mechanism. Conditional female choice for rare or transiently beneficial sires is predicted to arise under frequency-dependent selection on alternative ecological or competitive strategies, if females are able to incorporate information from social cues that predict the ecological or competitive conditions that their offspring are likely to face (Alonzo and Sinervo 2001). Although the production of unfertilized eggs is never an adaptive strategy, the rejection of sperm from low-quality sires is adaptive in the context of a system in which females are not sperm or mate limited. In our experiment, females were paired with only one male, but in the wild, female side-blotched lizards mate multiply and are not limited in access to potential sires (Zamudio and Sinervo 2000). Females of this species have previously been shown to adjust reproductive decisions in response to local morph frequencies (Comendant et al. 2003; Lancaster et al. 2007), and to exhibit adaptive patterns of sperm sorting following mating with multiple sires (Calsbeek and Sinervo 2002). These lines of prior evidence indicate that rejection of sperm from the single male that females were offered in the lab may reflect an adaptive sperm sorting strategy evolved in the wild, in which non-mate-limited females can isolate or handicap sperm of less-preferred males (Pizzari and Birkhead 2000). Alternatively, higher fertility when mated disassortatively (fig. 1A) may reflect nonadaptive prezygotic genetic incompatibilities arising within morphotypes (akin to inbreeding depression). Increased fertility when mated to conditionally high-quality males (fig. 1B) is less amenable to explanation by a nonadaptive genetic incompatibility hypothesis, as this pattern of fertility has clear fitness benefits under multiple paternity, and because conditionally high-fitness morphotypes are highly transient (switching every 1–2 years). The rapid buildup and erosion of transient, nonadaptive genetic incompatibilities within morphotypes in a pattern that happens to favor fertilization by conditionally high-quality males is plausible but less parsimonious in our view than cryptic female choice.

Fetal Viability Effects

In contrast to the fertility benefits of disassortative mating, fertile eggs produced through assortative matings had higher viability than those produced through disassortative mating (fig. 1C). Postzygotic reproductive incompatibilities are highly unlikely to reflect female choice, so this result suggests that genetic incompatibilities can arise among morphs in sympatry. Genetic incompatibilities between interbreeding morphs have been demonstrated in another color-polymorphic system, the Gouldian finches (Pryke and Griffith 2009), but those incompatibilities were thought to have arisen in allopatry. Our results are more surprising, considering that ancestral state reconstruction indicates that *Uta stansburiana* morphs have coexisted in sympatry for several million years (Corl et al. 2010). In related studies, Huyghe et al. (2010) found significant genetic differentiation at multiple microsatellite loci between ancestrally sympatric morphs of Dalmatian wall lizards, and Galeotti et al. (2013) found evidence for higher egg viability in some morphotype-assortative pairings of a congeneric wall lizard species. Together these results suggest that genetic divergence of alternatively selected alleles among morphotypes (i.e., under correlational selection), accompanied by weakly assortative mating, may be sufficient to invoke partial postzygotic reproductive isolation among morphs in sympatry.

Son Fitness Effects

We found that disassortative pairings did not always produce rare or high-fitness son morphotypes. In 2004, we found evidence that disassortative matings led to the expected production of rare, conditionally high-fitness son morphotypes. In 2006, however, conditionally high-fitness son morphotypes were more likely to be produced via assortative pairings (expected fitness of sons; table 2). This result derives from the particulars of the study system, in which the long-term average frequency of the O morphotype is lower than those of the B and Y morphotypes (0.16 vs. 0.40 and 0.44, respectively, averaged over 1990–2007; B. R. Sinervo et al., unpublished data). For sons of 2006 matings, O males had the lowest fitness (in 2007), and therefore males and females producing high fitness sons in 2007 (Y and B) were also relatively common in comparison to O males in 2006. The 2006 son fitness result demonstrates that departures of equilibrium morph frequency from equality (1 : 1 : 1) can affect departures from the predicted outcomes of frequency-dependent dynamics.

Agents of Selection

We found that disassortative matings with respect to morphotype produced higher rates of fertility and resulted in higher expected siring success of sons in one out of two years of our study. These results suggest that preexisting frequency-dependent selection on males (here representing alternative intrasexual selection strategies) favors disassortative mating in females, at least under some conditions, and females may respond by cryptically choosing sperm from disassortative matings. Our results also suggest that disassortative mating in this context is likely more strongly favored as equilibrium morph frequencies approach equality, but that this strategy may be less effective under more unequal long-term morph frequencies. We found that mating with conditionally high-quality males (i.e., males exhibiting morphotypes predicted to benefit sons) resulted in higher rates of fertility across both years of our study, suggesting that conditional mating preferences or patterns arising in response to preexisting frequency-dependent selection may not reflect a simple disassortative rule, and resulting fitness benefits of these conditional mating strategies could complement or counteract fitness consequences of disassortative or assortative matings.

We found that females accrue fitness benefits from mating assortatively via enhanced fertile egg viability, which may reflect higher egg survivorship when coadapted gene complexes are preserved. We did not identify any fertility outcomes consistent with cryptic choice for assortative pairings, but previous results indicate that females behaviorally prefer assortative matings (Bleay and Sinervo 2007). This raises the possibility that alternative female choice mechanisms (behavioral vs. cryptic) may have each evolved under different, conflicting selection pressures.

Despite the fact that we observed a fitness trade-off between assortative and disassortative mating outcomes consistent with conflicting selection pressures, we cannot rule out the possibility that the fitness effects we observed were caused at least in part by other sources, including genetic incompatibilities arising from allelic interactions at the OBY locus itself, for reasons unrelated to correlational or frequency-dependent selection. Regardless of the causes of conflicting fitness effects arising from assortative and disassortative matings, this conflict has consequences for the long-term balance between correlational and frequency-dependent selection in polymorphic populations. Resolution of the mating conflict in favor of either assortative or disassortative patterns may destabilize this balance, potentially leading to the breakup of coadapted gene complexes or destabilization of the polymorphism.

Conclusions

Correlational selection and frequency-dependent selection have each been considered important forces maintaining and shaping the distribution of genetic diversity within and between populations and species (Wright 1978; West-Eberhard 1986; Brodie 1992; Dybdahl and Lively 1998). However, multiple sources of diversity-promoting selection have rarely been considered together. We suggest that these two forces of selection should often act in tandem whenever polymorphisms involve multiple, unlinked traits. Interactions among these selection regimes may lead to conflicts and trade-offs that alter frequency-dependent dynamics and constrain the evolution of adaptations in the context of alternative morphotypes. Consideration of such interactions and conflicts among multiple forms of balancing and diversifying selection is necessary for a comprehensive understanding of how genetic diversity arises, is maintained, and is ultimately partitioned among populations and species.

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Male and female side-blotched lizards (*Uta stansburiana*). Photo credit: Lesley Lancaster.