

Population differences in condition-dependent sexual selection may promote divergence in non-sexual traits

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ABSTRACT

Hypothesis: Populations undergoing different patterns of condition-dependent sexual selection can diverge not only in the sexual signals directly targeted by selection, but also in correlated traits (e.g. body size or condition).

Organisms: Spadefoot toads (*Spea multiplicata*).

Methods: Because interactions with heterospecifics can affect the expression of mate choice, I compared the condition of females' preferred mates and randomly chosen unmated males between populations that differed in the presence of heterospecifics. I also determined experimentally whether these males' condition predicted offspring growth.

Results: Female mate choice may exert directional selection on male condition in allopatry but not sympatry: the condition of females' preferred mates was significantly higher in allopatry than in sympatry. Moreover, in allopatry, but not sympatry, the condition of preferred males predicted offspring growth. These population differences could explain, at least in part, why *Spea multiplicata* adults are larger and females more fecund in allopatry than in sympatry.

Keywords: fitness trade-offs, mate choice, mate-quality recognition, reproductive character displacement, sexual selection, speciation, species recognition.

INTRODUCTION

Female choice for good-condition males should generally promote the evolution of exaggerated male sexual signals, which are indicative of male condition (reviewed in Andersson, 1994; Tomkins *et al.*, 2004). An important implication of such mate choice is that when female preferences differ between populations, male sexual signals can also diverge. Indeed, divergent mate preferences may have contributed to the extraordinary diversity in sexual signals that we observe in nature (reviewed in Andersson, 1994).

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In contrast, relatively little attention has focused on the possibility that divergent mate choice patterns can generate population differentiation in traits not directly involved in sexual signalling (Pfennig and Pfennig, 2005). Yet, female choice for particular male signals can drive the correlated evolution of traits such as body size, condition, and non-sexual aspects of morphology. Moreover, if preferred male traits indicate a male's ability to sire offspring with enhanced fitness, female choice can indirectly promote in the population as a whole the evolution of better condition [depending on the genetic basis of condition (see review by Tomkins *et al.*, 2004)], larger body size (Pfennig and Pfennig, 2005), increased fecundity (Pfennig and Pfennig, 2005), faster development, and higher pathogen resistance. Thus, populations experiencing differing patterns of mate choice may diverge in traits that are not the direct targets of female choice.

A key means by which populations may diverge in female mate choice is reproductive character displacement – the evolution of divergent mating behaviours in sympatry versus in allopatry with a closely related heterospecific. Reproductive character displacement often occurs when natural selection favours the evolution of mating behaviours in sympatry (but not allopatry) that reduce hybridization (i.e. reinforcement) (Dobzhansky, 1940; Howard, 1993; Andersson, 1994; Servedio and Noor, 2003; Coyne and Orr, 2004). Although reproductive character displacement is generally well documented (reviewed in Howard, 1993; Servedio and Noor, 2003), less is known of its possible role in promoting divergence between populations in traits that are not direct targets of female mate choice.

Reproductive character displacement may often promote divergence between populations in non-sexual traits as an indirect consequence of population differences in sexual selection on condition-dependent traits. To illustrate how differences in condition-dependent selection between populations in sympatry and allopatry might arise, consider a situation in which allopatric females prefer males that possess exaggerated values of a condition-dependent trait, as is often the case for sexually selected characters (Andersson, 1994). Such males would likely provide females with either direct benefits that enhance their fecundity or survival or indirect 'good genes' benefits that increase their offspring's fitness (Andersson, 1994). When such females encounter heterospecifics (as would occur in sympatric populations), they might frequently hybridize if heterospecifics possess exaggerated versions of the signals that females prefer (Gerhardt, 1982; Ryan and Rand, 1993; Pfennig, 1998). If hybridization is costly, females in sympatry would be under selection to evolve preferences either for less exaggerated versions of the condition-dependent trait or for alternative traits that signal conspecific identity (Pfennig, 1998; Candolin, 2003; Hebets and Papaj, 2005; e.g. Gerhardt, 1994; Pfennig, 2000; Rosenthal *et al.*, 2002; Hankison and Morris, 2003; Gumm *et al.*, 2006). In either case, because newly evolved preferences in sympatry might not enable females to discern differences in condition among males, sympatric females may not receive benefits available to allopatric females who were able to assess male quality reliably (Pfennig, 1998, 2000). Moreover, female choice would no longer enforce a relationship between male condition and secondary sexual characters indicative of male condition (Rowe and Houle, 1996; Tomkins *et al.*, 2004). Consequently, the resulting differences between sympatry and allopatry in expression of condition-dependent sexual selection could in turn promote differentiation between allopatry and sympatry in traits such as body size or condition that are not necessarily the direct targets of female mate preferences (Pfennig and Pfennig, 2005). Indeed, the differential expression of condition-dependent sexual selection could generally increase mean population fitness and enhance rates of adaptation in allopatry relative to sympatry (*sensu* Lorch *et al.*, 2003).

I evaluated the role of reproductive character displacement in indirectly promoting divergence in non-sexual traits using spadefoot toads, *Spea multiplicata*. *Spea multiplicata* females co-occur and risk hybridization with a congener, *S. bombifrons*, in the southwestern USA. As I describe below, previous work indicates that *S. multiplicata* females give up the benefits of identifying good-condition conspecifics to avoid mating with *S. bombifrons*, thereby possibly reducing condition-dependent sexual selection in sympatry (Pfennig, 2000; see also Pfennig and Pfennig, 2005).

Hybridization with *S. bombifrons* appears costly for *S. multiplicata* females: male and female hybrids may have reduced fecundity (Simovich, 1985; Simovich *et al.*, 1991; but see Forester, 1975), and hybrid offspring of *S. multiplicata* females have lower survival and slower development relative to pure *S. multiplicata* tadpoles (Pfennig and Simovich, 2002). Because of these costs, *S. multiplicata* females likely have been under strong selection to avoid hybridization. Consequently, sympatric *S. multiplicata* females have evolved mate preferences that minimize their risk of hybridization (Forester, 1973; Pfennig, 2000) but which also preclude their ability to identify high-quality conspecific males (Pfennig, 2000). In allopatry, *S. multiplicata* females prefer male calls that have extreme call rates (Pfennig, 2000), a potentially condition-dependent character (Taigen and Wells, 1985; Prestwich *et al.*, 1989; Cherry, 1993; Grafe, 1996; Bevier, 1997). Moreover, where *S. bombifrons* is absent, *S. multiplicata* females preferentially mate with males that are heavier for a given body size and that provide them with enhanced fertilization success (Pfennig, 2000). By contrast, *S. multiplicata* females that co-occur with *S. bombifrons* prefer calls that are slower and more dissimilar from those of *S. bombifrons* and hybrid males (Pfennig, 2000) [hybrid males are possibly sterile (Simovich, 1985; Simovich *et al.*, 1991)]. Unlike allopatric females, sympatric *S. multiplicata* females do not identify males that are heavier for a given body size or that can provide them with enhanced fertilization success (Pfennig, 2000).

The trade-offs in mate choice decisions made by *S. multiplicata* females appear to have contributed, at least in part, to possibly pleiotropic effects on the evolution of body size (and, concomitantly, female fecundity) in sympatry versus allopatry: compared with adults in allopatry, those in sympatry are smaller, and females less fecund; the size disparity is especially pronounced for males (Pfennig and Pfennig, 2005). Indeed, sexual dimorphism in body size is inversely correlated with the frequency of *S. bombifrons* (Pfennig and Pfennig, 2005), as would be expected if avoidance of hybridization by *S. multiplicata* contributes to differences in sexual selection between sympatry and allopatry.

Whether and how differences in mate choice behaviour contribute to the evolved differences in body size between sympatry and allopatry remains unclear (Pfennig and Pfennig, 2005). If allopatric (but not sympatric) females preferentially mate with larger males that produce larger offspring, females may exert directional selection on body size. Alternatively, females may preferentially mate with males that are in better condition in allopatry but not sympatry. Such condition-dependent sexual selection may in turn promote indirect evolution of enhanced body size if good-condition males provide females with a good genes benefit of enhanced offspring growth.

In this study, I assessed whether and how trade-offs in mate choice behaviour contribute to the evolved differences in body size between sympatry and allopatry. Specifically, I determined whether *S. multiplicata* females exert directional selection on either male body size or male condition in allopatry but not sympatry with *S. bombifrons*. Additionally, I evaluated whether male size or condition predicts offspring size in allopatry but not sympatry. I found that trade-offs in mate choice decisions generate different patterns of

condition-dependent sexual selection in sympatry and allopatry that may ultimately contribute to differences in body size evolution between populations.

MATERIALS AND METHODS

The overall goal of this study was to determine if differences in mate choice behaviour could have generated the observed differences in body size between sympatry and allopatry. Specifically, I examined whether males can potentially sire offspring with better growth in allopatry but not sympatry, a pattern that could account for evolved differences in body size and fecundity between sympatry and allopatry (Pfennig and Pfennig, 2005). To do so, I analysed data from the following experiment [details of the design are also provided in Pfennig (2000)]. In two different years (1997 and 1998), I collected amplexed pairs (before gamete release) from a high-elevation, pure-species (i.e. allopatric) pond in which *S. multiplicata* was the only *Spea* species present [~1650 m elevation; *S. bombifrons* does not occur above 1500 m elevation (Simovich, 1985; Pfennig *et al.*, 2006)]. I also collected pairs from three lower-elevation, mixed-species (i.e. sympatric) ponds (~1200 m elevation) in which both *S. multiplicata* and *S. bombifrons* occur and risk hybridization. All ponds were within 10 km of each other near Portal, Arizona.

Upon capture, I immediately broke apart each pair and designated the male as that female's 'preferred' mate. Once I had completed the collection of pairs, I collected an equal number of unmated calling males from the same pond later on the same night. These males were designated 'non-preferred' males because they were calling (and therefore could have been assessed by females) but had not acquired a mate (*Spea* pairs remain amplexed throughout a breeding event, so that, once paired, males and females have a single mate during a breeding event).

I measured mass and snout-to-vent length for each preferred and non-preferred male. In a previous study (Pfennig, 2000), I controlled for snout-to-vent length in these mass measurements by correcting mass to the average male snout-to-vent length for each population type. Because the measures of males were standardized within each type of population, comparisons of condition could not be made across populations. Thus, for this study, I used as a measure of male condition the residuals of a cubic regression of mass on snout-to-vent length for all preferred and non-preferred males collected ($F_{3,58} = 66.7$, $P < 0.0001$, $R^2 = 0.78$; the residuals were normally distributed). Higher positive values of the residuals mean that males are heavier than expected given the relationship between mass and snout-to-vent length, and could have greater energy reserves. I could therefore compare this measure (using *t*-tests) between preferred and non-preferred males within and across sympatry and allopatry.

On the same night the above pairs were collected, I paired each female to both her original preferred mate and a randomly chosen non-preferred male from her same breeding aggregation. To do so, I placed each female in 13.5 litres of dechlorinated water with either her preferred mate or a non-preferred male. Whether the female was first mated to her preferred mate or to a non-preferred male was randomly determined. After each female released half her clutch (*Spea* have external fertilization), I separated her from her first mate, rinsed her with water to remove residual sperm, and placed her with her second mate.

Once mating was completed, I removed a random subset of hatchlings from each clutch and reared them to metamorphosis in wading pools of 1.8 m diameter (Pfennig, 2000). Within each wading pool, I placed two mesh-sided boxes (1.0 × 0.7 × 0.2 m), each of which

contained offspring from a single female: one box contained 25 tadpoles sired by the female's preferred mate and the other contained 25 tadpoles sired by her randomly assigned non-preferred male. I fed tadpoles in each box rabbit chow three times for a total of 10.59 g per box, thereby simulating detritus on which tadpoles feed in natural ponds (Pfennig *et al.*, 1991). In 1997, I measured mass and snout-to-vent length of surviving tadpoles at first forelimb emergence (average age at which tadpoles were measured was 34 days). In 1998, I measured surviving tadpoles when they were between 35 and 37 days old or at first forelimb emergence, whichever came first (average age at which tadpoles were measured was 35 days). For each box, I calculated the mean size of all tadpoles (in most boxes all tadpoles survived; no box had fewer than 10 surviving tadpoles).

In my previous study (Pfennig, 2000), I compared offspring growth between preferred and non-preferred males within each population using paired *t*-tests. I found no differences in mean growth between preferred and non-preferred males in sympatry or allopatry, a result that may have been due, in part, to lack of power in the experimental design. In that previous study, however, I did not determine if male size or condition predicted offspring growth. Thus, to do so for this study, I regressed offspring growth on the size and condition for each male type (preferred from allopatry, non-preferred from allopatry, preferred from sympatry, and non-preferred from sympatry) separately. Because some data points were potential outliers, I also used randomization tests (using Rndom Projects 2.01 LITE) to relate offspring growth to male size as above. Because the results from these analyses replicated the findings of the parametric analyses, I report only the parametric results here.

RESULTS

My goal was to determine if trade-offs in mate choice behaviour associated with reproductive character displacement could contribute to differences in adult body size between sympatry and allopatry. One explanation for differences in adult body size between sympatry and allopatry is that females in allopatry, but not sympatry, preferentially mate with larger males that sire larger offspring. However, I found no evidence to support this hypothesis. Although allopatric preferred (P) and non-preferred (NP) males were significantly larger in adult body size than their counterparts in sympatry [P: mean difference allopatry – sympatry (\pm S.E.) = 4.98 (0.88) mm, $t_{29} = 5.64$, $P < 0.0001$; NP: mean difference allopatry – sympatry (\pm S.E.) = 6.39 (1.23), $t_{29} = 5.22$, $P < 0.0001$], females did not appear to choose males on the basis of body size *per se*. In both allopatry and sympatry, preferred males were not different from non-preferred males in snout-to-vent length [allopatry: mean difference NP – P (\pm S.E.) = 0.58 (0.85) mm, $t_{26} = 0.68$, $P = 0.50$; sympatry: mean difference NP – P (\pm S.E.) = -0.83 (1.18), $t_{32} = -0.71$, $P = 0.48$]. Moreover, size of preferred or non-preferred males did not predict offspring size in either allopatry or sympatry (sympatric NP: $F_{1,15} = 0.19$, $P = 0.67$; sympatric P: $F_{1,15} = 0.09$, $P = 0.77$; allopatric NP: $F_{1,12} = 0.59$, $P = 0.46$; allopatric P: $F_{1,12} = 0.0001$, $P = 0.99$).

Alternatively, differences in adult body size between sympatry and allopatry could be explained, in part, by differences in condition-dependent sexual selection between sympatry and allopatry. Indeed, preferred males were in significantly better condition than non-preferred males in allopatry, but not sympatry, as was found previously (see Methods) using a slightly different analysis of these data [allopatry: mean difference NP – P (\pm S.E.) = -1.17 (0.52), $t_{26} = -2.26$, $P = 0.03$; sympatry: mean difference NP – P (\pm S.E.) = -0.09 (0.34), $t_{32} = -0.27$, $P = 0.79$] (see also Pfennig, 2000).

These results suggest that female choice may exert directional selection on male condition in allopatry but not in sympatry. Consistent with this hypothesis, allopatric preferred males were in significantly better condition than sympatric preferred males [mean difference allopatry – sympatry (\pm s.e.) = 1.12 (0.40), $t_{29} = 2.80$, $P = 0.009$]. In other words, males that were mating successfully and siring offspring were in better condition in allopatry than in sympatry. This pattern was not observed among the non-preferred males, which were not significantly different in condition between sympatry and allopatry [mean difference allopatry – sympatry (\pm s.e.) = 0.04 (0.45), $t_{29} = 0.09$, $P = 0.93$].

When I evaluated whether male condition predicted offspring growth for the different male types from sympatry and allopatry, I found that condition did not predict offspring size for either sympatric non-preferred males ($F_{1,15} = 0.88$, $P = 0.36$; Fig. 1A) or for sympatric preferred males ($F_{1,15} = 0.03$, $P = 0.87$; Fig. 1B). Male condition of allopatric non-preferred males also did not predict offspring size ($F_{1,12} = 0.03$, $P = 0.86$; Fig. 1C). Only for preferred males in allopatry did male condition predict offspring size ($F_{1,12} = 5.08$, $P = 0.04$; Fig. 1D).

DISCUSSION

I sought to evaluate whether reproductive character displacement can generate differences in the expression of condition-dependent sexual selection that contribute to divergence of traits that evolve indirectly via mate choice. I focused on spadefoot toads, which undergo reproductive character displacement in sympatry with a heterospecific congener (Pfennig, 2000). I specifically asked whether females exert directional selection on male size and condition in allopatry but not in sympatry. I also investigated whether males can potentially sire offspring with better growth in allopatry but not sympatry, a pattern that could account for evolved differences in body size and fecundity between sympatry and allopatry (Pfennig and Pfennig, 2005).

My findings revealed that mate choice might contribute to increased offspring growth in allopatry but not in sympatry. In allopatry, females appeared to identify good-condition males that could provide them with indirect benefits of enhanced offspring growth. By contrast, in sympatry, females did not appear to identify good-condition males that could provide such a benefit (contrast Fig. 1B with Fig. 1D). Because offspring growth may predict adult body size, these differences in condition-dependent sexual selection could account for the larger body size of *Spea multiplicata* in allopatry versus sympatry.

One alternative explanation for these observed differences in condition-dependent mate choice is that males are more variable in allopatry than in sympatry (contrast Figs. 1C and 1D with Figs. 1A and 1B). Consequently, females may have been better able to discriminate among males in allopatry versus sympatry. Yet, the choice of males with elaborate secondary signals that reveal condition in allopatry may increase male variance relative to males in sympatry where females exert stabilizing selection on male secondary signals and forego information regarding male condition (Gerhardt, 1991; Pfennig, 2000; Shaw and Herlihy, 2000). Thus, whether population differences in variation among males are a cause or an effect of the different patterns of condition-dependent sexual selection requires further study.

A drawback of this study is that the relationship between male condition and offspring growth was only measured in three sympatric populations and in a single allopatric population. Additional work will be needed to evaluate whether the findings can be generalized beyond these populations and also to assess whether confounding ecological factors may

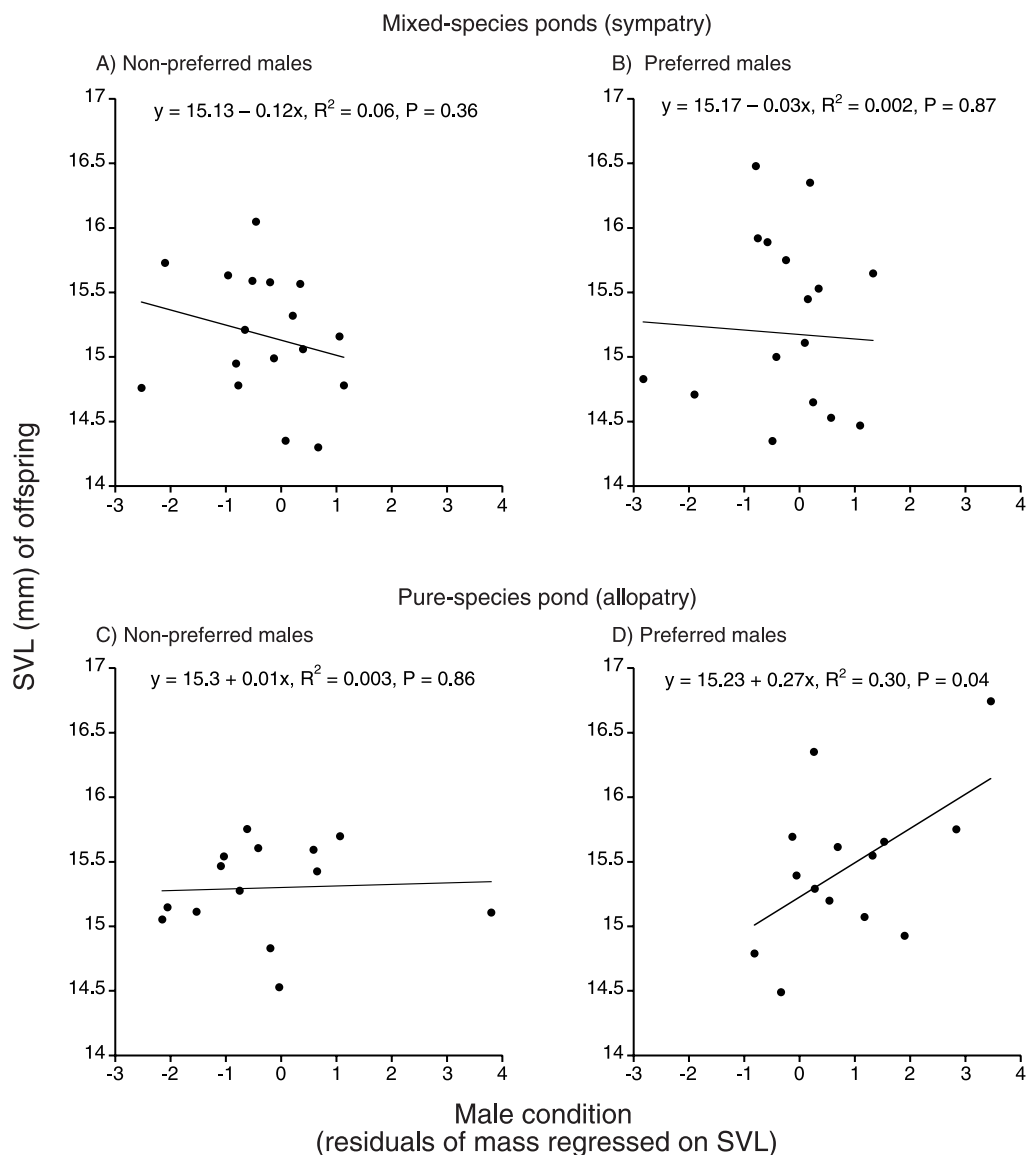


Fig. 1. Relationship between paternal condition and offspring body size (snout-to-vent length, SVL) for offspring sired by: (A) non-preferred (NP) males in mixed-species (sympatric) ponds (where both *S. multiplicata* and *S. bombifrons* occur); (B) preferred (P) males in mixed-species (sympatric) ponds; (C) non-preferred males in a pure-species (allopatric) pond (where only *S. multiplicata* occurs); and (D) preferred males in a pure-species (allopatric) pond. Each point represents the mean of at least 10 offspring. Randomization tests with these data produced the same outcome as shown by the parametric analyses (see text).

explain the differences between these populations. Specifically, elevation is confounded with differences in the presence of heterospecifics between sympatric and allopatric populations. Yet, the differences in body size that are observed between sympatry and allopatry, which

may have arisen from the patterns of sexual selection reported here, are associated with the presence of *S. bombifrons*, not elevation (Pfennig and Pfennig, 2005). Indeed, the expression of sexual dimorphism in body size in a population, a measure of sexual selection, is correlated with the frequency of *S. bombifrons* in that population (Pfennig and Pfennig, 2005). Taken together, these multiple lines of evidence suggest that the presence of heterospecifics, rather than other ecological factors (e.g. elevation), likely alters the expression of condition-dependent sexual selection in sympatry versus allopatry. Moreover, the present results, combined with previous findings (Pfennig and Pfennig, 2005), indicate that the way in which female mate choice evolves via reproductive character displacement may have important implications for how conspecific populations diverge in traits beyond those directly involved in mate choice.

Why did condition predict offspring growth only for the allopatric preferred males? In spadefoots, where fertilization is external and males provide no parental care, the relationship between male condition and offspring growth is most likely mediated by a genetic effect (i.e. 'good genes'). Thus, allopatric preferred males may be those who possess alleles that best enable them to allocate resources to condition, and, when conferred to offspring, these alleles are also responsible for enhancing offspring growth.

This finding is consistent with the notion that female choice for exaggerated, condition-dependent traits may generate positive covariance among male condition, the expression of condition-dependent signals, and the ability of males to confer good genes benefits to females [i.e. genic capture (Rowe and Houle, 1996; Lorch *et al.*, 2003; Tomkins *et al.*, 2004)]. Indeed, the finding that condition predicted offspring growth only for allopatric preferred males suggests that, in allopatry, female choice may promote a relationship between male condition and offspring quality that in turn further enhances selection on females to identify males of better condition. In contrast, in sympatry, where females do not select males on the basis of condition [see Results and also Pfennig (2000)], covariance between male signals and condition (and, concomitantly, male ability to provide good genes to offspring) should break down because males who allocate resources to sexual signalling would no longer be favoured. That sympatry may be undergoing this countervailing pattern of 'genic release' relative to the process of genic capture that may be underway in allopatry has two key implications. First, these contrasting processes would only serve to exacerbate further the costs of the trade-off that sympatric females may experience when they forego mating with high-quality males to ensure conspecific matings (see also Pfennig, 2000). Second, the opposing patterns of condition-dependent selection would exaggerate possible differences between the two population types in the evolutionary trajectories of male condition, sexual signals, female choice, and the traits with which they are correlated.

Sexual selection is often expected to reduce population fitness (Lande, 1980; Kirkpatrick, 1982; Grafen, 1990; Kirkpatrick and Ryan, 1991; Tanaka, 1996). The results presented here, however, suggest that, when females ensure mating with conspecifics at the expense of identifying good-condition mates, population fitness may actually be reduced in the absence of condition-dependent sexual selection. Adults are smaller in sympatry than in allopatry (Pfennig and Pfennig, 2005) and, because of the reduced size of females in sympatry, they also have reduced fecundity (Pfennig and Pfennig, 2005). That condition of mated males predicts offspring size in allopatry but not sympatry may explain these differences in body size (and the concomitant reduction in fecundity) between sympatry and allopatry. Because larger size at the larval stage may persist into adulthood in anurans (Altwegg and Reyer, 2003), differences in the ability of males to produce large offspring may explain, at least in part, why adults in allopatry are

larger than adults in sympatry (Pfennig and Pfennig, 2005). Moreover, because condition may fuel enhanced growth, male size may experience a correlated increase with increases in condition.

These findings are consistent with recent theory, which indicates that condition-dependent sexual selection can increase mean population fitness and enhance the rate of adaptation in populations experiencing such selection versus those that do not (Lorch *et al.*, 2003). Indeed, because recruitment may be lower in sympatric populations (e.g. due to reduced fecundity and/or lower survivorship of smaller larvae and adults), sympatric populations that experience reduced sexual selection on condition-dependent characters may be more prone to ‘Darwinian extinction’ – extinction events that result when adaptive trade-offs reduce mean population fitness and, consequently, population viability (Webb, 2003; Pfennig and Pfennig, 2005). Thus, trade-offs in mate choice decisions brought about by reproductive character displacement may have far-reaching implications for the divergent evolution in sympatry versus allopatry of non-reproductive traits (e.g. body size and condition), mean population fitness, and population viability.

Finally, this study highlights the trade-offs in mate choice that may evolve when females are faced with the risk of costly hybridization, and emphasizes the possibility that reproductive character displacement may require that females give up fitness benefits that are potentially available to allopatric females. Ultimately, this trade-off may enhance the likelihood that sympatric and allopatric conspecific populations may diverge and, eventually, become reproductively isolated from one another. Recent studies have suggested that reproductive character displacement can promote speciation among conspecific populations if mating signals become so divergent between allopatric and sympatric populations that females fail to recognize migrant males as mates (Hoskin *et al.*, 2005; Pfennig and Ryan, 2006). Yet, why mating behaviour should diverge between sympatry and allopatry to the point that migrants have reduced mating success in either population is not always clear. Trade-offs in mate choice could produce this pattern by generating opposing patterns of signal evolution and mate choice in sympatry versus allopatry. Consequently, migrants of either sex may be expected to have lower fitness than residents in either population type. Thus, although trade-offs in mate choice behaviour that arise as a consequence of reproductive character displacement may owe their origins to speciation processes such as reinforcement, these trade-offs may in turn contribute to speciation as well.

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