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ORIGINAL ARTICLE

A condition-dependent male sexual signal predicts adaptive predator-induced plasticity in offspring

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Abstract

The possibility that sexual selection promotes adaptive evolution in variable environments remains controversial. In particular, where the scale of environmental variation results in parents and their offspring experiencing different environmental conditions, such variation is expected to break down associations between adult sexual traits and adaptive offspring traits. However, when adaptive offspring plasticity in nonsexual traits acts as an indirect benefit of mate choice, then mate choice for males that produce more plastic offspring could promote adaptation to variable environments. This hypothesis assumes that male sexual signals predict offspring plasticity, which has rarely been tested. To test this assumption, we used spadefoot toads (*Spea multiplicata*) to investigate whether variation in male sexual signals predicts the expression of tadpole tail-fin plasticity in response to predation cues. Such plasticity has been shown to be adaptive in numerous amphibian taxa. We found that condition-dependent male call characteristics predicted offspring plasticity. Generally, both phenotypic plasticity and female mate choice are ubiquitous in nature; therefore, adaptive associations between male sexual signals and offspring plasticity such as the one reported here might be common.

Significance statement

Sexual signals can indicate individuals' capacity to sire high-quality offspring, which provides a mechanism by which sexual selection can contribute to adaptive evolution. Whether this occurs in variable environments is unclear, however, because variable environments can expose parents and their offspring to different selection pressures. To address this uncertainty, we investigated the possibility that sexual signals can signal the capacity to sire offspring that express adaptive phenotypic plasticity in response to prevailing selective pressures. Using spadefoot toads, we found that condition-dependent male sexual signals predict the expression of tadpole tail-fin plasticity in response to predation cues. Because this form of plasticity has been demonstrated to be adaptive in several amphibian taxa, our results suggest that associations between sexual signals and adaptive offspring plasticity can allow sexual selection to promote adaptive evolution in variable environments.

Keywords Local adaptation · Mate choice · Phenotypic plasticity · Sexual selection · Spadefoot toads · Tadpoles

Introduction

Can sexual selection promote adaptation, especially in variable environments? Theory predicts that mate preferences for exaggerated, condition-dependent sexual signals can promote adaptation by generating adaptive associations between sexual traits (mate preferences and sexual signals) and offspring fitness (Proulx 1999; Proulx 2002; Lorch et al. 2003; Tomkins et al. 2004; Cotton et al. 2006; Veen and Otto 2015; Servedio and Boughman 2017). Yet other theory conversely predicts that environmental variation can generate mismatches between adult sexual traits and offspring phenotypes and fitness, which can preclude sexual selection from promoting adaptation in variable environments (Qvarnström 2001; Bussiere et al. 2008; Kokko and Heubel 2008; Cornwallis and Uller 2009; Miller and Svensson 2014). However, if sexual signals predict adaptive offspring plasticity, then mate preferences for such signals will favor the production of offspring that can express adaptive phenotypes under prevailing environmental conditions, even if those conditions differ from

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those experienced by the parents. In other words, adaptive phenotypic plasticity in offspring could constitute a fitness benefit of mate choice, and sexual selection via mate choice for plastic offspring could thereby promote adaptation to variable environments (Kelly et al. 2019).

The hypothesis that offspring plasticity could function as a fitness benefit of mate choice rests on conventional predictions of mate choice theory (sensu Andersson 1994). In particular, because direct assessment of potential mates' capacity to produce high-quality offspring is unlikely (Andersson 1994), sexual signals should reliably indicate potential mates' capacity to produce adaptively plastic offspring. Further, for such signals to remain honest indicators of the ability to produce plastic offspring, they should be condition dependent or otherwise costly to produce (Zahavi and Zahavi 1999; Achorn and Rosenthal 2020). Yet, despite the potential for sexual signals to indicate whether a prospective mate can produce adaptively plastic offspring, few studies have examined this possibility.

We therefore sought to determine whether a form of adaptive tadpole plasticity that is widespread among amphibians is predicted by male sexual signals in spadefoot toads, *Spea multiplicata*. Specifically, we tested whether male sexual signals predict the expression of tadpole tail-fin plasticity in response to cues that signal the possible presence of predators. This type of tadpole plasticity occurs among diverse amphibian taxa (e.g., Smith and Van Buskirk 1995; Van Buskirk and Schmidt 2000; Relyea 2002; LaFiandra and Babbitt 2004; Kraft et al. 2005; Michimae and Hangui 2008; Touchon and Warkentin 2008), and experiments using multiple taxa have demonstrated that such plasticity is adaptive (e.g., McCollum and Van Buskirk 1996; Van Buskirk et al. 1997; Van Buskirk and McCollum 1999; McIntyre et al. 2004; Kraft et al. 2006). In particular, tadpoles develop deeper tails in response to predator cues, which facilitates escape; however, deeper tails are associated with slower growth and so are disfavored in the absence of predators (McCollum and Van Buskirk 1996; Van Buskirk et al. 1997; Van Buskirk and McCollum 1999; McIntyre et al. 2004; Relyea 2004; Kraft et al. 2006). We found that *S. multiplicata* tadpoles developed deeper tail fins in response to predation cues and that this plasticity is associated with both male (sire) body condition (size-adjusted mass) and male sexual signals (calling effort). Thus, offspring plasticity might function as an indirect benefit of mate choice and allow sexual selection to facilitate adaptation in variable environments.

Material and methods

Study System

Spea multiplicata occur in dry areas of southwestern North America (Bragg 1965; Dodd 2013). They typically breed once annually in ephemeral, rain-filled ponds (Pfennig 1990, 1992a, 2007). Males call to attract females, and females choose their mates on the basis of their call characteristics, primarily call rate (calls per minute) (Bragg 1965; Pfennig 2000). In most populations, females prefer relatively high-condition males that produce relatively rapid call rates, which are associated, in turn, with higher fertilization success and enhanced offspring growth (Pfennig 2000, 2008). Females choose their mates by closely approaching and touching a male, which initiates pair formation (Pfennig 2000).

Spea tadpoles exhibit resource-use polyphenism: they can develop a default "omnivore" phenotype with generalized trophic morphology or, as a result of intense intraspecific competition and ingestion of live prey, develop an inducible "carnivore" phenotype with trophic morphology specialized for catching and consuming live prey (Pfennig 1990, 1992a, b). This polyphenism is a product of negative frequency-dependent selection (Pfennig 1992a; Skulason and Smith 1995; Pfennig and Pfennig 2012). Importantly, equilibrium frequencies of carnivores vary within and across generations (Pfennig 1992a, b; Martin and Pfennig 2009, 2010, 2012). This variable frequency-dependent selection therefore favors the capacity for tadpoles to assess their environment and respond accurately by developing either the omnivore or carnivore phenotype via plasticity (Pfennig 1990, 1992a, b; Martin and Pfennig 2009, 2010, 2012).

In this study, we chose to evaluate the capacity for omnivore tadpoles to express tail-fin plasticity. We did not use carnivore tadpoles for the following reasons. Tadpoles that express the carnivore phenotype feed on Anostracan fairy shrimp and other tadpoles, including conspecifics (Pfennig 1990, 1992b; Pfennig et al. 1993). Carnivore tadpoles are likely the primary source of predation on omnivore tadpoles (Pfennig et al. 1993), although predation by other predators, such as Odonate naiads, occurs as well (Pomeroy 1981). Thus, both the sources and intensity of predation on omnivore tadpoles are variable, which should favor omnivore tail-fin plasticity. Further, if omnivore *S. multiplicata* tadpoles express tail-fin plasticity in response to predation on conspecifics, a likely inducing cue is the presence of injured conspecifics (i.e., an "alarm cue" sensu Schoeppner and Relyea 2005), rather than a predator-specific cue. Thus, we used injured conspecific cues as a proxy for predation in our experiment (see below).

Field collections and tadpole rearing

At a natural breeding aggregation on the night of 01 August 2019 at approximately 22:00 h in southeastern Arizona, USA (31°55′10.8" N, 109°09′40.2" W), we individually recorded 10 calling *S. multiplicata* males for approximately one minute and then collected them. The water temperature at the time of recording was 16.25 °C. Males at the breeding aggregation had been calling for at least 2 h before we began recording. One-minute recordings are sufficient to capture representative variation in this continuously calling species: *S. multiplicata* males produce 31 calls per minute on average, and the duration of each call is 1.1 s on average (Pfennig 2000), and comparisons with longer recordings show no effect of recording length on measures of male call parameters (G. Calabrese and KSP, unpublished data). Moreover, in Arizona, *S. multiplicata* breed on a single night in a given population, with both male calling and female mate choice occurring in the span of several hours; therefore, variation in which males attend a given aggregation (i.e., the male competitive environment) and night-to-night variation in temperature do not confound mate choice (Bragg 1965; Pfennig 2000). In addition, the 10 males that we recorded and collected represented more than half of all males calling at the breeding aggregation; as is common for *S. multiplicata* (Bragg 1965; Pfennig 2000), this aggregation consisted of fewer than 20 calling males, which were surveyed without difficulty in the small pond in which the aggregation formed. We measured all males for snout-to-vent length (SVL) and mass. We also collected 10 female *S. multiplicata* at the same aggregation.

Immediately following collection, we randomly paired each recorded male with a female for breeding in separate tanks filled with 6 L of dechlorinated well water at the Southwestern Research Station. After approximately 8 h, upon visual confirmation that oviposition had occurred, we removed the adults from the tanks and began aerating the eggs. Approximately 48 h later, after all tadpoles had hatched and begun swimming, we provided each tank with 20 mg of crushed detritus (TetraFin® Fishfood Pellets), which mimics the natural diet of omnivore tadpoles and does not induce expression of the carnivore phenotype (Pfennig et al. 2006). We continued daily feedings of 20 mg detritus per tank for 3 days and then increased to 40 mg daily for the subsequent 3 days. On the sixth day after tadpoles hatched, we transported the tadpole sibships via automobile in their respective rearing tanks to UNC Chapel Hill, which took 3 days during which we provided 40 mg of detritus per tank twice daily. We did not quantify mortality during transport, but very few tadpoles died during transport, and we did not observe differences among the sibships in mortality. We also transported the adult *S. multiplicata* used in the breedings to UNC for addition to the colony housed there.

Experimental methods

At UNC, we set up six replicate microcosms (34 × 20 × 12 cm plastic boxes with 6 L dechlorinated tap water) per sibship. We designated three microcosms per sibship as controls, and the remaining three microcosms for each sibship comprised our treatment group. Each microcosm contained 10 visually size-matched siblings, such that each sibship had 30 tadpoles per treatment (starting total $N = 600$ tadpoles). Visual inspection unambiguously confirmed that no tadpoles expressed the carnivore phenotype. On days one through nine of the experiment, we provided each microcosm 100 mg detritus daily, and on days ten through twelve, we provided each microcosm 120 mg detritus daily. We kept the remainder of each sibship in their original rearing tanks for use as stimuli (see below). We provided each original rearing tank 120 mg detritus daily for the duration of the experiment.

On days two though twelve, we applied our injured conspecific cue to the treatment group. To do so, we selected six tadpoles from each sibship's original rearing tank and euthanized them in a 0.1% aqueous solution of tricaine methanesulfate (MS-222). Then, we crushed them, thoroughly rinsed them with dechlorinated water to remove MS-222, and used a dipnet to place two per microcosm in each of the corresponding sibship's three treatment microcosms. On days three through twelve, we removed the previous day's crushed tadpoles from each treatment microcosm before adding fresh ones (there was very little consumption of the crushed tadpoles, and growth did not differ between control and treatment groups; see the "Results" section). In addition, on days two through twelve, we disturbed the water in the control microcosms with a clean, empty dipnet in a manner that simulated placing crushed tadpoles in the treatment microcosms.

On day 13, we euthanized all experimental tadpoles in MS-222 (we also euthanized all remaining tadpoles in the original rearing tanks). Immediately after euthanizing them, we photographed the tadpoles from a lateral point of view using a Canon digital SLR camera and 50-mm macro lens. After photography, we stored the euthanized tadpoles in 95% ethanol. Owing to mortality, our final sample size was 496 tadpoles (240 in the control group and 256 in the cue group).

To minimize observer bias, we had a trained observer perform all tadpole measurements without knowledge of the experimental protocol or microcosm designations. The observer used ImageJ to measure SVL and maximum tail depth (ventral maximum of ventral fin to dorsal maximum of dorsal fin) for each tadpole.

Call analyses

We used the computer program Audacity to calculate two condition-dependent temporal characteristics of male calls. The first, call rate, has previously been shown to predict tadpole phenotypes and fitness (Pfennig 2000, 2008; Kelly et al. 2019). The second, call effort, is commonly used as a proxy for "vocal performance," or the energetic expenditure made by male frogs while calling (Ward et al. 2013; Lee et al. 2017). We calculated call rate as calls per minute, and we calculated call effort as the product of call rate multiplied by call duration (i.e., mean call length in seconds) (Ward et al. 2013; Lee et al.

2017). To minimize observer bias, we used blinded methods when performing call analyses.

Statistical analyses

We performed all analyses using R (R Core Team 2019). To account for tadpole tail depth allometry, we used residuals from a linear regression of ln tadpole tail depth on ln tadpole SVL in place of raw tail depth measurements.

To determine whether *S. multiplicata* tadpoles developed deeper tail fins in response to the injured conspecific cue, we used a linear mixed effects model in the R package lmerTest (Kuznetsova et al. 2017). Our response variable was SVL-corrected tail depth, and our fixed effects were treatment (control or cue) and sibship. To test for a genotype-by-environment (GxE) effect, we also included the interaction of treatment and sibship as a fixed effect. We specified replicate as a random effect, and we used an *F* test with Kenward-Roger approximations to degrees of freedom for inference. In addition, to assess whether growth differed between treatments, we used a linear mixed effects model with SVL as the response variable and treatment as the fixed effect. For random effects, we specified sibship and replicate. We again used an *F* test with Kenward-Roger approximations to degrees of freedom for inference.

To determine whether sire condition and/or call characteristics predicted the expression of tail-fin plasticity, we calculated a plasticity index for each sibship. We calculated this index as Hedge's g effect sizes for each sibship's response to the experimental treatment. Hedge's g consists of the difference in treatment means (each sibship's mean SVL-corrected tail depth in the control versus cue treatments) divided by the pooled weighted standard deviation (the square root of the sum of the squared standard deviations from each treatment divided by two). Hedge's g is very similar to Cohen's d but performs better with small sample sizes (Hedges and Olkin 2014). Next, we calculated male (sire) body condition as the scaled mass index (SMI), which adjusts mass for a given SVL via standardized major axis regression (Peig and Green 2009). Then, we regressed the plasticity index on sire call rate, call duration, call effort, and condition (in separate regressions). In addition, to test for condition dependence of call characteristics, we regressed them on male condition.

Finally, we used logistic regression in a generalized linear mixed effects model to determine whether mortality differed among cue and control groups or among sibships. We first specified treatment, sibship, and the interaction of those terms as fixed effects and replicate as a random effect, but no models that included sibship converged. However, a model with sire call effort and treatment as fixed effects and replicate as a random effect converged, and we report that model below. We additionally report models with sire call rate, call duration, and body condition (SMI) substituted for call effort (in separate models), with all other model terms unchanged. We used Wald chi-squared tests for inference.

Results

Tadpoles developed deeper tail fins in the treatment group than in the control group ($F_{1,30.927} = 8.334$, $P = 0.007$; Fig. 1). This effect was independent of body size: we corrected tail depth for SVL, and we did not detect an effect of treatment on SVL in a mixed model ($F_{1,8.477} = 1.701$, $P = 0.226$). Thus, *S. multiplicata* exhibit plastic responses to predation (in the form of injured conspecific cues) like those of other amphibian taxa. In addition, we found GxE effects on tail depth (treatment-by-sibship interaction: $F_{1,38.72} = 7.412$, $P = 0.010$; Fig. 2).

Male body condition (SMI) predicted the expression of tadpole tail-fin plasticity ($F_{1,8} = 17.460$, $R^2 = 0.65$, $P = 0.003$; Fig. 3b). In particular, males with relatively high body condition sired tadpoles that exhibited the greatest tail-fin plasticity.

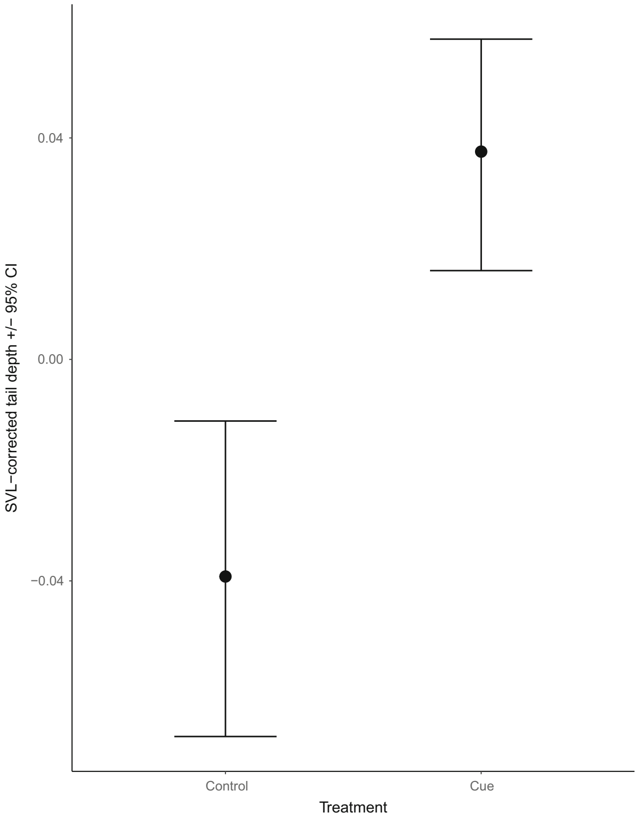

Fig. 1 Mean SVL-corrected tail depth with 95% bootstrapped CI for all tadpoles reared in the control and cue treatments. Bootstrapping was performed with 1000 simulations in the "boot" function of the R package boot (Canty and Ripley 2020). SVL-corrected tail depth consists of residuals from the regression of ln tail depth on ln SVL

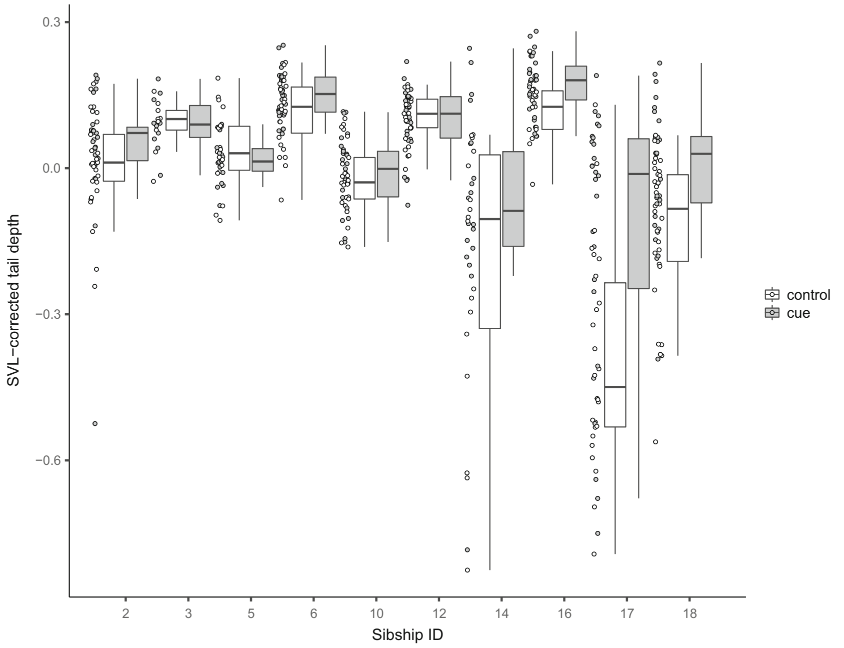

Fig. 2 SVL-corrected tail depths (points) and box-and-whisker plots for each sibship and each treatment. Points are immediately to the left of their corresponding box-and-whisker plots. The box-and-whisker plots are as follows: thick black lines represent the medians, boxes represent the interquartile ranges, and whiskers extend to the most extreme points within 1.5 × the interquartile ranges outside the boxes. SVL-corrected tail depth consists of residuals from the regression of ln tail depth on ln SVL. Sibships are displayed in numerical order of their identifying numbers from the experiment. Points are jittered slightly on the *x* axis

Call rate did not predict the expression of tadpole tail-fin plasticity ($F_{1,8} = 0.036$, $P = 0.854$), but call effort did ($F_{1,8} = 7.319$, $R^2 = 0.41$, $P = 0.027$; Fig. 3a). Males that exhibited relatively high call effort sired tadpoles that exhibited the greatest tail-fin plasticity. This relationship appears to be driven primarily by call duration; males with longer call durations sired tadpoles with greater tail plasticity ($F_{1,8} = 8.669$, $R^2 = 0.46$, $P = 0.019$). Further, although condition did not predict call rate ($F_{1,8} = 0.001$, $P = 0.983$), it did predict call effort ($F_{1,8} = 6.998$, $R^2 = 0.40$, $P = 0.030$) and call duration ($F_{1,8} = 7.232$, $R^2 = 0.41$, $P = 0.028$), consistent with call effort being a condition-dependent call character.

We did not detect an effect of treatment on tadpole mortality ($\chi^2 = 0.441$, DF = 1, $P = 0.507$), but sire call effort predicted tadpole survival. Specifically, tadpoles sired by males with higher call effort were likelier to survive to the end of the experiment ($\chi^2 = 4.857$, df = 1, $P = 0.0275$). No other sire characteristics predicted survival (call rate: $\chi^2 = 1.251$, df = 1, $P = 0.263$; call duration: $\chi^2 = 0.061$, df = 1, $P = 0.805$; body condition (SMI): $\chi^2 = 0.057$, df = 1, $P = 0.811$).

Discussion

An association between adult sexual traits and offspring plasticity can maintain the relationship between sexual traits and offspring fitness that is required if sexual selection promotes adaptive evolution in variable environments. We investigated a key assumption of this hypothesis by evaluating whether male call characteristics predict the expression of a taxonomically widespread form of tadpole plasticity. We showed that tadpoles of our study species, *Spea multiplicata*, develop deeper tails in response to a proxy for predation: injured conspecific cues (Fig. 1). Further, we found that both male body condition and call effort predicted the expression of tadpole tail-fin plasticity in response to injured conspecific cues. Specifically, higher condition males with higher call effort sired tadpoles that exhibited greater plasticity in tail-fin depth (Fig. 3). Although some might contend that our sample size (10 sires) was small, the 10 males sampled represented the majority of males calling in the population that we sampled (see above). Furthermore, our results are consistent with published data showing that male *S. multiplicata* call characteristics predict adaptive plasticity in other tadpole traits (Kelly et al. 2019). Importantly, the present study details not merely a similar predictive relationship between call characteristics and tadpole plasticity, but one that involves a form of plasticity that is common among diverse amphibian taxa (Touchon and Robertson 2018).

Indeed, the existence of similar forms of sexual signaling among anuran taxa (Wells 2010) and the broad taxonomic distribution of this form of tadpole tail plasticity suggest that offspring plasticity might commonly maintain adaptive associations between sexual traits and offspring fitness in variable environments. In particular, the capacity to develop deeper tail fins in response to injured conspecific or predator cues has been demonstrated to be adaptive in the context of predator avoidance in multiple anuran taxa (e.g., McCollum and Van Buskirk 1996; Van Buskirk et al. 1997; Van Buskirk and McCollum 1999; McIntyre et al. 2004; Kraft et al. 2006). Further, although we did not measure tadpole fitness as a function of tail plasticity, the cue that we used in our

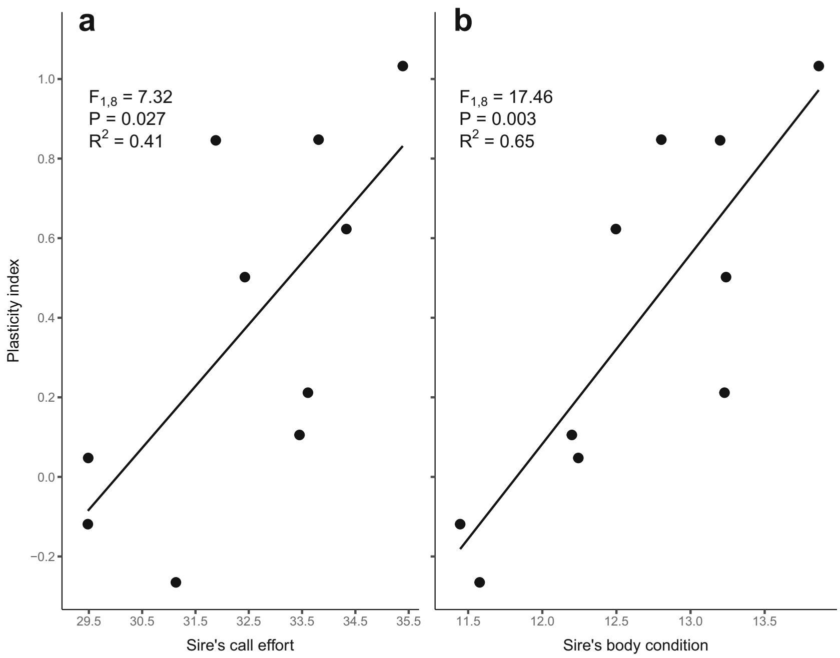

Fig. 3 **a** Linear regression of tadpole plasticity on sire call effort (the product of call rate [calls/min] multiplied by call duration [sec]). Slope estimate = 0.156 +/− 0.058 (1 SE). **b** Linear regression of tadpole plasticity on sire body condition (body condition = standardized mass index, which adjusts mass for a given SVL). The plasticity index consists of Hedge's g effect sizes; higher values indicate greater plasticity, i.e., greater difference between mean SVL-corrected tail depth in the cue treatment compared to control (see the "Material and methods" section for further details). Slope estimate = 0.477 +/− 0.114 (1 SE)

experiment is likely a reliable indicator of predation risk in this system (Pomeroy 1981; Pfennig et al. 1993). Therefore, the plasticity demonstrated here is likely adaptive.

That the adaptive offspring plasticity is associated with male call effort and body condition suggests that it could function as an indirect fitness benefit of mate choice. Previous work has found that females prefer faster calling males but show no discrimination between male calls that differ in duration (Pfennig 2000). In these preference tests, only one call feature was manipulated at a time; all other call characters were controlled. However, females have not been tested for their preferences of call effort per se, and preferences for call rate and call duration might interact in ways that have not been captured in previous studies. Thus, whether females use call effort to choose mates who sire offspring with greater tail plasticity is an open question. However, we additionally found that male call effort predicted tadpole survival in this experiment, which suggests that females may benefit from choosing to mate with high-call-effort males nonetheless.

Interestingly, although male call rate did not predict tadpole tail-fin plasticity, call rate does predict another form of tadpole plasticity; namely the likelihood of expressing the carnivore morph (Kelly et al. 2019). Different components of frog calls are often indicators of different phenotypes, such as species identity, fecundity, body condition, or offspring characteristics (Wells 2010). Moreover, female frogs are known to assess multiple call components (Gerhardt 1991, 1994; Pfennig 2000; Wells 2010). It is therefore plausible that different components of *S. multiplicata* calls communicate different offspring characteristics, including different forms of plasticity. This possibility requires further research.

Our finding that both male call effort and body condition predict the expression of tadpole tail-fin plasticity further suggests the possibility that mate preferences for condition-dependent signals can facilitate adaptation in variable environments. Generally, because plasticity is likely to mediate offspring fitness in variable environments (Whitman and Agrawal 2009), only those offspring capable of facultatively expressing adaptive phenotypes in a given environment are likely to achieve the condition necessary to producing preferred sexual signals (sensu Proulx 1999; Proulx 2001; van Doorn et al. 2009). This type of condition dependence is central to theoretical models that suggest that mate choice can promote adaptation because it couples nonsexual fitness with sexual traits (Proulx 1999, 2001; van Doorn et al. 2009; Veen and Otto 2015; Servedio and Boughman 2017). Our results suggest that offspring plasticity can mediate such associations and allow sexual selection to promote adaptation in variable environments.

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Authors' contributions DWP, PWK, and KSP conceived of the study. PWK performed field recordings and collections, the experiment, and the analyses. PWK drafted the manuscript with help from DWP and KSP. All authors revised and approved the manuscript.

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Data availability Data from this study are available via DRYAD (DOI: 10.5061/dryad.t4b8gtj0w).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval All procedures were approved by UNC's IACUC (IACUC ID 20-016.0 and 20-036.0). Field collections were performed in accordance with permits granted by the Game and Fish Departments of Arizona and New Mexico. All applicable international, national, and/or institutional guidelines for the use of animals were followed.

Consent to participate Not applicable.

Consent to publish Our manuscript is not under consideration for publication elsewhere, and all authors have seen and approved the manuscript for submission. All persons entitled to authorship have been so named.

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