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Male sexual signal predicts phenotypic plasticity in offspring: implications for the evolution of plasticity and local adaptation

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In a rapidly changing world, understanding the processes that influence a population's ability to respond to natural selection is critical for identifying how to preserve biodiversity. Two such processes are phenotypic plasticity and sexual selection. Whereas plasticity can facilitate local adaptation, sexual selection potentially impedes local adaptation, especially in rapidly changing or variable environments. Here we hypothesize that, when females preferentially choose males that sire plastic offspring, sexual selection can actually facilitate local adaptation to variable or novel environments by promoting the evolution of adaptive plasticity. We tested this hypothesis by evaluating whether male sexual signals could indicate plasticity in their offspring and, concomitantly, their offspring's ability to produce locally adapted phenotypes. Using spadefoot toads (*Spea multiplicata*) as our experimental system, we show that a male sexual signal predicts plasticity in his offspring's resource-use morphology. Specifically, faster-calling males (which are preferred by females) produce more plastic offspring; such plasticity, in turn, enables these males' offspring to respond adaptively to the spadefoots' highly variable environment. The association between a preferred male signal and adaptive plasticity in his offspring suggests that female mate choice can favour the evolution and maintenance of phenotypic plasticity and thereby foster adaptation to a variable environment.
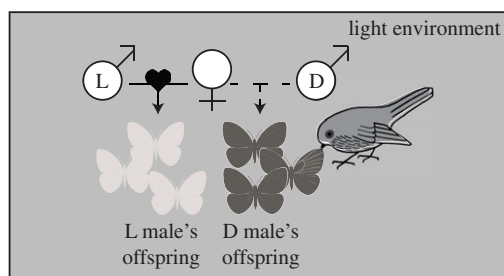
This article is part of the theme issue 'The role of plasticity in phenotypic adaptation to rapid environmental change'.
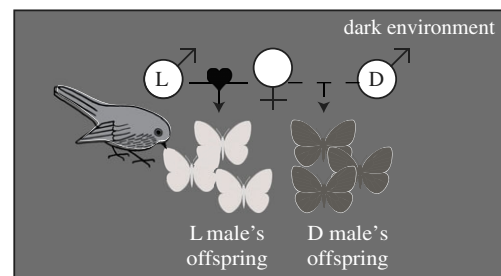
1. Introduction

In an ever-changing world, environmental fluctuations preclude any one phenotype from being consistently favoured by natural selection [1]. To cope with these fluctuations, organisms have evolved numerous strategies to generate adaptive phenotypic variation [2]. One such widely used strategy is phenotypic plasticity (hereafter, simply 'plasticity')—the ability of an individual organism to change its phenotype in direct response to stimuli or inputs from the environment [3,4]. Although not all plasticity is adaptive [5], 'adaptive plasticity' (i.e. plasticity that enhances the bearer's fitness [6]) enables organisms to respond to environmental variability by expressing phenotypes that are selectively favoured under prevailing conditions, even when these conditions change unpredictably [3,7].

An open question, however, is whether and how plasticity impacts *evolution*. On the one hand, some researchers argue that plasticity only impedes evolution [8]. According to this viewpoint, if a single genotype can produce multiple phenotypes in response to changing environmental conditions, then such plasticity should shield populations from a strong directional selection [9]. On the other hand, a growing number of researchers maintain that plasticity can play a leading and decisive role in evolution [3,10–22]. For example, if underlying genetic

Figure 1. (a) How sexual selection (as mediated by female mate choice) impedes local adaptation in rapidly changing environments. Generally, females should possess preferences for males who sire offspring with locally adapted traits. For instance, females that occur in a light environment in which visually oriented predators are present should prefer males that sire light-coloured offspring ('L' males) over males that sire dark-coloured offspring ('D' males). However, in a rapidly changing environment (in this case, one that changes into a dark environment), a formerly adaptive preference might become maladaptive. Here, the formerly adaptive light-coloured offspring sired by the 'L' male are now more likely to be detected by predators. (b) When females preferentially choose males that sire plastic offspring, sexual selection can facilitate local adaptation to rapidly changing environments. In this case, males that sire plastic offspring ('P' males) should produce more surviving offspring than either L or D males (who sire non-plastic offspring) across both environments (note that we have assumed here that plastic offspring bear a cost not borne by non-plastic offspring in the environment for which they are adapted; weakening this assumption only increases the advantage to P males).
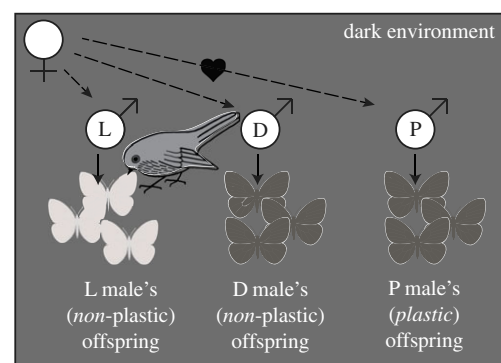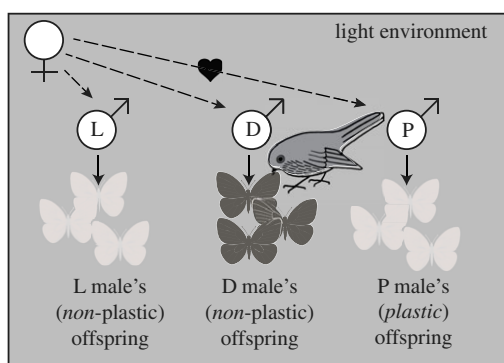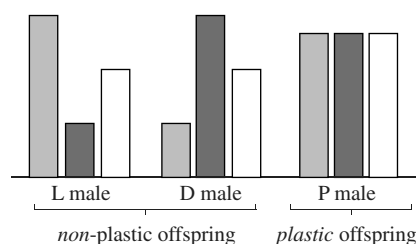
variation exists in either the tendency or manner in which individuals respond to the environment (i.e. if different genotypes exhibit different 'reaction norms,' as is nearly always the case [23,24]), then selection can act on this variation—revealed to selection through plasticity—and refine the expression of the affected trait such that it is optimally suited to local conditions [3]. In this way, plasticity can facilitate local adaptation [25–27].

Like plasticity, sexual selection—the differential mating success of individuals stemming from competition for mates [28]—has been proposed to both facilitate and impede adaptive evolution [28–31]. Although there are numerous ways in which sexual selection can promote adaptation [31], it has long been regarded as an impediment to adaptive evolution in rapidly changing environments [32,33]. In such situations, sexual selection can generate an evolutionary momentum that maintains patterns of mating behaviours that, while they may have enhanced local adaptation to some past environment, result in the production of maladaptive offspring in the altered environment (figure 1a). In other words, in

ever-changing environments, females might often harbour preferences for males who sire offspring that are locally disfavoured by natural selection. Although these females would likely be under strong selection to adopt new preferences for males who produce offspring that are favoured in the changed environment [34,35], there will likely be a time lag before such selection promotes the evolution of either new preferences or the sexual signals that indicate a male's ability to sire offspring that are adaptive in the altered environment. During this time lag, populations might have lower mean fitness and even a higher risk of extinction [36,37]. Moreover, populations in constantly changing environments might be perpetually in this state of 'evolutionary time lag,' in which females continually express preferences for mates who sire offspring that are maladapted to the prevailing environment, thereby causing sexual selection to inhibit local adaptation.

These arguments assume that females have *fixed* preferences. However, individual females can modify their mate choice preferences in direct response to prevailing conditions

Table 1. Alternative routes whereby sexual selection can impact the evolution of phenotypic plasticity.

route	description of route
plasticity in secondary sexual traits	(1) competitively mediated, disruptive, intra-sexual selection can favour the evolution of alternative condition-dependent (plastic) secondary sexual traits (e.g. ornaments, signals, weapons) [42–44]. (2) variation in the environment can favour plastic expression of sexual signals that: a) are more readily detected by females in that environment; or b) better indicate male quality (ability to confer fitness benefits to females or their offspring) in the given environment [45].
plasticity in mate choice	(1) if the fitness consequences of mate choice vary depending on circumstances, selection will favour condition- or context-dependent female preferences or choosiness. Indeed, in many species, female choice is sensitive to variation in factors such as parasites, predators, season, and the female's diet, social status and age [39,40]. (2) in variable environments (or where choice is costly), selection can favour females that copy the mate preferences of other females (e.g. older or more successful females) or that learn preferences based on environmental exposure [40].
choice for mates that sire plastic offspring	female mate choice favours the evolution of plasticity in offspring when they prefer males that sire plastic offspring [see §3].

[38–40]. These 'context-dependent preferences' (*sensu* [39]) are a form of plasticity, and they allow females to choose mates who sire offspring with adaptive traits, even in rapidly changing environments. Such plasticity is widespread, and it is expected to evolve if females can detect cues from the environment that reliably predict the environmental context that their offspring will experience [39–41].

However, females cannot always reliably assess the environment that their offspring will encounter. Such a situation might be especially likely to arise when the environment changes rapidly (i.e. within an individual's lifetime) and unpredictably. In these circumstances, females could produce adaptive offspring by preferring males who sire *offspring that are themselves plastic*. In particular, selection could favour females that prefer mates who produce offspring that can assess and respond adaptively to their local environment through plasticity. As a consequence of such preferences, sexual selection would facilitate local adaptation. Moreover, because plasticity is typically favoured in variable environments [3,7], sexual selection (specifically, mate choice) could also operate in tandem with natural selection to promote the evolution of plasticity.

This notion that mate choice itself might promote plasticity is especially intriguing. Indeed, although researchers have long recognized that sexual selection can shape the evolution of plasticity via multiple routes (e.g. by favouring the evolution of condition-dependent female preferences or male signals; table 1), the possibility that sexual selection might favour plasticity's origin and maintenance has rarely been considered. Yet, clarifying whether sexual selection can favour the evolution of plasticity is important, not only for understanding the conditions under which sexual selection can facilitate local adaptation in variable environments but also for understanding how plasticity itself evolves.

Here, we evaluated these ideas empirically by using spadefoot toads, *Spea multiplicata*, as our model system. As we explain below, in this species, female mate choice mediates sexual selection on male sexual signals [46–48]. Moreover, the offspring develop in highly variable environments that

favour plasticity; consequently, the tadpoles produce a novel environmentally induced resource-use phenotype as an alternative to their default tadpole morphology [49–51]. Using an experimental approach, we specifically evaluated whether: (1) a male sexual signal (that is known to be preferred by females) predicts the degree and quality of expression of the induced resource-use morphology; (2) the preferred male sexual signal predicts plasticity in the production of the induced morphology versus the alternative default morphology; and (3) the preferred male sexual signal predicts offspring fitness such that more plastic offspring have enhanced fitness relative to less plastic offspring.

Our results indicate that the preferred male sexual signal does indeed predict: the expression of environmentally induced resource-use morphology in offspring; the extent of plasticity in that morphology versus the default morphology; and the resulting fitness of that plasticity. Critically, females are known to prefer males with the sexual signals that we found are indicative of greater plasticity and higher offspring fitness. Consequently, our results suggest that sexual selection can facilitate adaptation by promoting the evolution of plasticity.

2. Material and methods

(a) Study system and specific goals

Mexican spadefoot toads, *Spea multiplicata*, occur in the desert scrub and desert grasslands of northern Mexico and the southwestern USA. In these regions, annual rainfall is concentrated in July and August, when localized thunderstorms fill highly ephemeral ponds that vary in depth and duration, both spatially and temporally [41,49,50]. Spadefoot toads breed, and their tadpoles develop, in these ephemeral ponds.

Spea breed on a single night following pond filling [46,52]. Males call to attract mates, and females choose their mates by initiating pair formation when they closely approach and touch the male [46]. Sexual signalling and mate choice in any one population take place over a few hours; thus, mate choice is not

confounded by variation in which males attend an aggregation on a given night or by nightly variation in environmental factors such as temperature [46,52].

In populations where they do not risk hybridizing with a congener (S. bombifrons), female S. multiplicata prefer males with faster call rates that are in better condition [46–48,53]. By preferring such males, females choose mates that provide them with higher fertilization success and enhanced growth in offspring [46,47].

Spea multiplicata tadpoles express alternative, environmentally induced resource-use phenotypes [49,50]. Specifically, tadpoles develop into either an 'omnivore' ecomorph, a round-bodied tadpole with a long intestine, small jaw muscles and smooth keratinized mouthparts, or a 'carnivore' ecomorph, a narrow-bodied tadpole with a short intestine, greatly enlarged jaw muscles and serrated mouthparts. Omnivores are dietary generalists that feed on detritus, algae and small crustaceans; carnivores are dietary specialists that feed mostly on anostracan fairy shrimp and other tadpoles [54].

Development of these alternative ecomorphs is underlain by phenotypic plasticity. Spea tadpoles are born as omnivores, but if a young individual consumes fairy shrimp or other tadpoles, it may develop into the carnivore phenotype [49,55]. However, families differ in the propensity to produce carnivores when fed shrimp or tadpoles, suggesting underlying genetic variation in ecomorph production and, hence, in the expression of phenotypic plasticity [56,57]. Additionally, males appear to differ in the *quality* of carnivore offspring that they sire, as indicated by their trait integration; i.e. the nature of the correlations among different component traits of the carnivore morph [58] (see §2(b) below).

These alternative ecomorphs have presumably evolved as an adaptive response to pond ephemerality, resource availability and variation therein [49,50,59]. Owing to pronounced variation in rainfall, resource availability and tadpole (i.e. competitor) density across time and space, the ponds in which S. multiplicata tadpoles develop are rapidly changing, often unpredictable environments [49,50,59]. The carnivore ecomorph is generally favoured in dry years and in ponds with high shrimp densities: by specializing on high-nutrition shrimp and tadpole prey, the carnivore ecomorph develops faster than the omnivore ecomorph and thus is more likely to metamorphose and escape a rapidly drying pond [49,50]. In longer-duration ponds, however, frequency-dependent selection, which arises from intraspecific competition for dietary resources, maintains both ecomorphs at an equilibrium frequency within the same pond, and this equilibrium value is set by a given pond's relative availabilities of low-nutrition resources (i.e. detritus, algae and small crustaceans) versus high-nutrition resources (i.e. shrimp and other tadpoles) [50].

Moreover, disruptive selection also acts in these ponds [60]: individuals with phenotypes that are intermediate between the two ecomorph types suffer low relative fitness, likely owing to an inability to compete effectively with tadpoles expressing more extreme omnivore or carnivore phenotypes [61,62]. Thus, while the phenotypic plasticity underlying these alternative phenotypes results in continuous variation between them, almost all populations exhibit significantly bimodal distributions of the ecomorphs [59,60]. This, in combination with competition driving frequency-dependent selection and the high variability of pond environments, favours accurate assessment of environmental cues and the capacity to produce each ecomorph (and not intermediate phenotypes) [61,62].

Spadefoot natural history makes them particularly well-suited to evaluate whether male sexual signals that are preferred by females indicate plasticity in their offspring and, concomitantly, their offspring's ability to produce locally adapted phenotypes. To do so, we carried out two experiments aimed at evaluating whether or not a male sexual signal (i.e. call rate) predicts: (1) production and quality of the environmentally induced carnivore morphology of his offspring (i.e. how carnivore-like his offspring were when fed shrimp), and (2) the degree of plasticity in resource-use morphology expressed by his offspring (i.e. how different his offspring were in carnivore versus omnivore morphology when fed shrimp versus detritus).

(b) Does a male sexual signal predict offspring resource-use morphology?

We determined if male call rate predicts the production of carnivores among his offspring when they were fed shrimp exclusively (the resource type that induces the carnivore ecomorph and for which the carnivore ecomorph is best adapted to use [61]). We also asked whether male call rate predicts the fitness and trait integration of these carnivores. We used trait integration as a measure of the quality of carnivore phenotypes produced (see [58]).

We began by recording nine calling males at a natural breeding aggregation in an ephemeral pond (Crater) near Portal, Arizona, USA. In this pond, S. multiplicata is the only Spea species present. The nine recorded males represented the majority of males observed calling in this aggregation and they were all recorded within an hour (so rates are not affected by differences in temperature, male assembly or time of night). Each male was individually recorded by approaching him within 0.5 m using standard procedures [46] developed for this system. After recording a male's call for at least 1 min, each male was captured with a hand-held dip net and placed in an individually labelled container. The recordings were subsequently analysed for call rate; i.e. the number of calls per minute.

We then collected females from the same breeding aggregation and on the same evening. To collect females, we used hand-held dip nets to capture amplexed pairs as they formed. We immediately broke the pairs apart to recover the female. Collecting females in this way ensured that all females in the experiment were ready to breed. Once collections were complete, we returned the animals to the nearby Southwestern Research Station and immediately paired each female at random with one of the nine recorded males.

We placed each male–female pair in a water-filled tank and allowed them to breed naturally. The resulting eggs were aerated until tadpoles hatched. One day after hatching, we removed a subset of the tadpoles from each clutch and placed them in groups of five siblings in a microcosm (a 34 × 20 × 12 cm plastic box filled with 6 l of dechlorinated well water). We reared tadpoles in groups to assess the propensity and degree to which each family's tadpoles expressed the carnivore phenotype (rearing tadpoles on a shrimp diet in groups induces more extreme carnivores, presumably because of competition [63]). For each family, we replicated these microcosms 24 times, so that we had a total of 192 microcosms (24 microcosms per family × 8 families) for a total starting sample size of 1080 tadpoles. Each microcosm received a unique ID for use in our analyses (see below).

On Day 1 of the experiment, we provided each microcosm with equal amounts of detritus (TetraFin® Fishfood Pellets). These pellets simulated the detritus on which S. multiplicata tadpoles feed in the wild [64]. After Day 1, we began the carnivore-induction feeding regimen. Specifically, on Days 2–5 of the experiment, the tadpoles in each microcosm were provided daily with approximately 150 small, live fairy shrimp (Streptocephalus sp. or Thamnocephalus sp.). On Days 6–8, the tadpoles in each microcosm were provided daily with approximately 60 large, live fairy shrimp. All shrimp were obtained from a nearby, natural pond. On Day 9, the tadpoles were euthanized by immersion in a 0.1% aqueous solution of tricane methanesulfonate (MS 222) and preserved in 95% ethanol. Some tadpoles died in the experiment, and some samples were destroyed during transport, so our final sample size was 973 tadpoles.

To assess tadpole resource-use morphology, we measured the preserved tadpoles using previously published methods [62]. Specifically, we measured the width of each tadpole's orbito-hyoideus muscle (OH; carnivores have a larger OH) and scored its mouthparts (MP) on an ordinal scale that ranged from 1 (most omnivorous) to 5 (most carnivorous). We also counted the number of denticle rows (DR; omnivores have higher DR counts) and gut coils (GC; omnivores have a longer gut, which manifests as higher GC counts). After correcting OH for body size (by regressing ln OH on ln snout–vent length (SVL)), we combined these four measures into a single morphological index (MI; e.g. see ref. [56] and references therein). To calculate this index, we used a principal component (PC) analysis. The MI consisted of the first principal component (the PC with an Eigen value greater than 1), which explained 51.2% of the variance in resource-use morphology among our tadpoles. Larger values of the MI correspond to more carnivore-like tadpoles, with larger OH muscles, fewer DR and GC, and more serrated, notched mouthparts (higher MP scores). By contrast, smaller values correspond to more omnivore-like tadpoles, with smaller OH muscles, higher DR and GC counts and smoother mouthparts.

As proxies for fitness, we measured each tadpole's Gosner developmental stage (GS; [65]), body size (SVL) and mass. GS is an appropriate fitness proxy because faster-developing tadpoles are more likely to escape the highly ephemeral ponds in which *S. multiplicata* develop [49,50]. SVL and mass are also appropriate fitness proxies because larger body size is positively correlated with fitness in *S. multiplicata*. Larger tadpoles are more likely to survive to metamorphosis [53] and sexual maturity (D. Pfennig 2018, unpublished data). Larger tadpoles also mature as larger adults (D. Pfennig 2018, unpublished data), and adult body size, in turn, is positively correlated with mating success in males [46] and fecundity in females [53]. Finally, we measured body size of each adult male and female used in these breedings to account for any effects of parental body size on offspring morphology or fitness [66,67].

To analyse the data, we used a linear mixed-effects model with MI as the response variable, ln call rate as the fixed effect and family ID and replicate (microcosm) ID as random effects. The inclusion of the tadpoles' parents' body size did not improve the model (likelihood ratio test, $p = 0.57$). Therefore, parent body size was not included in subsequent analyses. To address propensities to develop as carnivores, we used a generalized linear model (GLM) with the total number of extreme carnivores (those with the highest MP scores among all tadpoles in the experiment [56]) sired by each male as the response variable and ln call rate as the predictor; we specified a Poisson distribution to account for the response consisting of count data. We also used family-level mean values of GS, SVL and mass in regressions on male call rate to assess whether male call rate predicts the fitness of his offspring.

Finally, prior work suggests that the presence of potential competitors (i.e. individuals in the same microcosm) can impact trait integration in the form of the strength of the correlation between OH and GC [58]. Specifically, a stronger, more-negative correlation between OH and GC indicates better trait integration because wider OH muscles are best suited for handling carnivore prey [56], whereas a long gut (i.e. greater GC counts) is best suited to digesting the low-nutrition omnivore diet [56]. Thus, a more-negative correlation between these two traits—for both the omnivores and carnivores—is indicative of a potentially better-performing phenotype overall [56,58]. Therefore, we calculated Pearson correlation coefficients for this pair of traits within each family and then regressed these family-specific coefficients on male call rate. In this latter analysis, a family with a relatively fast call rate was more extreme than others. An outlier analysis did not identify this family as a statistical outlier. Nevertheless, we used a non-parametric Spearman rank-order correlation analysis (which is not influenced by outliers) on the data. This non-parametric analysis produced results that were qualitatively the same as the parametric results, so we report the results from the parametric analysis.

(c) Does a male sexual signal predict offspring plasticity?

The above experiment evaluated whether male signals predict the production of the carnivore morphology. However, production of the carnivore morphology among different males' offspring might be at least in part genetic rather than being entirely environmentally induced. Thus, the 'default' morph (i.e. the phenotype produced at birth) might be more carnivore-like in some families than in others. Indeed, previous studies have shown that different families vary in their propensity to produce carnivores [56,57], and a related *Spea* species shows evidence that some tadpoles are actually born as carnivores [68]. We therefore sought to determine whether male call rate predicts *plasticity* in his offspring's resource-use morphology across two diets: a detritus diet (that should produce the omnivore ecomorph) and a shrimp diet (that induces the carnivore ecomorph).

We recorded 12 males at a different natural breeding aggregation from that used in §2b. This aggregation occurred in a temporary pond (PO2-N) between Portal, Arizona and Rodeo, New Mexico, USA. As in the experiment above, *S. multiplicata* was the only *Spea* species present, and the number of males recorded represented approximately one third of the males observed calling in this particular aggregation. Using the same procedures described above, we recorded males, paired them with females collected from their same breeding aggregation and produced families of tadpoles.

On the first day after the tadpoles hatched, we provided each tank with 20 mg of detritus as above. The following day, we placed tadpoles from each clutch individually in a microcosm (a 475 ml plastic cup filled with 400 ml of dechlorinated well water; rearing tadpoles singly eliminated competition, thereby allowing us to assess each tadpole's morphological responses to dietary cues alone). We randomly selected 60 tadpoles per family and divided them between two diet treatments: one in which tadpoles received only detritus (and thus developed more omnivore-like morphology), and one in which tadpoles received only fairy shrimp (the ingestion of which can induce development of the carnivore ecomorph [49,55]). Our starting sample size was 720 tadpoles (60 tadpoles × 12 families). Rearing cups were placed in equal-sized groups on shelves in a single room, with a shrimp-fed and a detritus-fed group from each family on each shelf (to account for any variation in temperature in the room).

Tadpoles fed on detritus received 10 mg of crushed fish food each on Day 1 and every second day thereafter. Shrimp-fed tadpoles received approximately 20 live fairy shrimp each on Day 1; this quantity increased by approximately 10 shrimp per day through Day 6. On Days 7–9, shrimp-fed tadpoles received live fairy shrimp ad libitum. All fairy shrimp were from natural ponds. On Day 10, we euthanized all tadpoles by immersion in MS 222 and preserved them in 95% ethanol. After some mortality, our final sample size was 706 tadpoles. Using the methods described above, we calculated an MI for each tadpole (in this experiment, MI [PC1] explained 53.4% of variance). As above, we also measured each tadpole's GS, SVL and mass. Additionally, we measured the body size (SVL) of the adult males and females used in the breedings to account for any effects of parental body size on offspring morphology or fitness.

To assess the relationship between male call rate and tadpole resource-use morphology, we used a linear mixed-effects model with MI as the response variable and ln call rate, diet, and the interaction of call rate and diet as fixed effects, and family ID
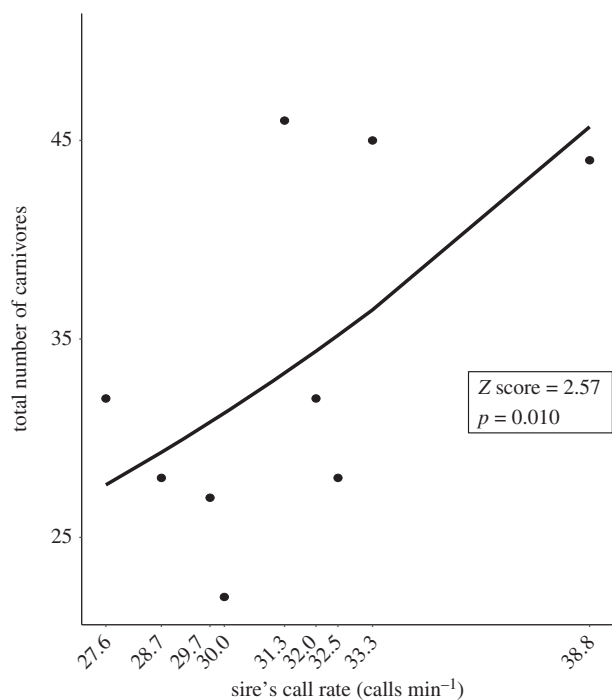
Figure 2. Generalized linear model fit with ln call rate (back-transformed) as the predictor and total number of carnivores as the response (Poisson distribution specified).

and group ID as random effects. The inclusion of adult body size did not improve the model (likelihood ratio test, $p = 0.84$), so those measures were not included in our final analysis.

Additionally, to assess plasticity in resource-use morphology, we calculated mean MI values for each family on each diet and then subtracted each family's mean MI on the detritus (omnivore) diet from its mean MI on the shrimp (carnivore) diet. We used a linear regression of this measure of plasticity on male call rate to determine the relationship between these two variables. To assess family differences in propensities to develop as carnivores, we summed the number of extreme carnivore phenotypes (those with the highest MP score among all tadpoles reared on the shrimp diet [56]) and used a GLM with Poisson distribution specified (to account for the response being count data) with family total number of carnivores as the response variable and male call rate as the predictor variable. Finally, we used family-level mean values of GS, SVL and mass in regressions on male call rate to assess differences in fitness proxies (for an explanation of these fitness proxies, see the description of the previous experiment above).

3. Results

(a) Does a male sexual signal predict offspring resource-use morphology?

Faster-calling males produced significantly more carnivores than slower-calling males (GLM with a Poisson distribution; Z score = 2.57, $p = 0.010$; figure 2). Faster-calling males also tended to produce tadpoles with more extreme carnivore morphology (as measured by MI; t-test with Satterthwaite approximations; $t = 1.90$, $p = 0.059$).

When we evaluated whether male call rate directly predicted offspring growth, we found no evidence that this was the case across all tadpoles (mass: $F_{1,7} = 4.64$, $R^2 = 0.31$, $p = 0.068$; SVL: $F_{1,7} = 3.11$, $p = 0.121$; GS: $F_{1,7} = 1.48$, $p = 0.263$). Nevertheless, male call rate predicted tadpole quality in

terms of trait integration. In particular, male call rate predicted the strength of a negative correlation between two key traits that impact tadpole performance: OH muscle size and gut length (as measured by GC). Specifically, tadpoles sired by males with faster call rates had stronger, more-negative correlations between OH muscle width and GC counts ($F_{1,7} = 8.13$, $R^2 = 0.47$, $p = 0.025$). Moreover, the strength of this correlation between OH and GC predicted tadpole size (mass: $F_{1,7} = 20.13$, $R^2 = 0.71$, $p = 0.003$; SVL: $F_{1,7} = 11.6$, $R^2 = 0.57$, $p = 0.011$).

(b) Does a male sexual signal predict offspring plasticity?

Diet treatments predicted offspring growth, development and resource-use morphology as expected. In particular, tadpoles reared on the shrimp diet grew larger, developed more quickly and exhibited more carnivore-like phenotypes than tadpoles reared on the detritus diet (Wilcoxon rank-sum tests; SVL: $p < 0.001$; mass: $p < 0.001$; GS: $p < 0.001$; MI: $p < 0.001$).

Male call rate predicted plasticity in his offspring's resource-use morphology. In particular, our linear mixed-effects model revealed a significant interaction between diet and male call rate ($t = 3.02$, $p = 0.003$). Whereas male call rate had no relationship with offspring MI on the detritus diet ($t = -1.64$, $p = 0.44$), call rate positively predicted offspring MI on the shrimp diet: males with faster calls sired offspring with more extreme carnivore MI scores ($t = -3.28$, $p = 0.007$); males with faster call rates also produced significantly more carnivores (Z score = 1.97, $p = 0.048$). That faster-calling males sired more plastic tadpoles was corroborated by differences between family-mean MI scores for shrimp- and detritus-reared tadpoles: call rate positively predicted larger differences in MI between the two diets ($F_{1,10} = 11.87$, $R^2 = 0.48$, $p = 0.007$; figure 3; see also figure 4).

Across diets, we found no evidence that male call rate predicted tadpole size or growth rate (SVL: $F_{1,10} = 2.52$, $p = 0.144$; mass: $F_{1,10} = 1.86$, $p = 0.203$; GS: $F_{1,10} = 0.519$, $p = 0.488$). However, when we excluded a single outlier family, faster-calling males produced significantly larger (but not faster-developing) offspring (SVL: $F_{1,9} = 10.86$, $R^2 = 0.50$, $p = 0.009$; mass: $F_{1,9} = 9.23$, $R^2 = 0.45$, $p = 0.014$; GS: $F_{1,9} = 4.02$, $p = 0.076$).

4. Discussion

We evaluated whether sexual selection and phenotypic plasticity interact to promote local adaptation in variable environments. In particular, we sought to determine whether females could use male sexual signals as an indicator of adaptive offspring plasticity. As we highlight below, female mate choice for males that sire plastic offspring could both promote local adaptation to variable or changing environments and favour the evolution and maintenance of plasticity.

Using spadefoot toads as our study system, we found that a male sexual trait (male call rate) predicted the expression of environmentally induced resource-use morphology (i.e. a distinctive carnivore ecomorph) in the male's offspring (figure 2). We also found that male call rate predicted the degree of trait integration in his offspring as well as the degree of plasticity in the expression of his offspring's resource-use morphology (figures 3 and 4). Previous work, focusing on the same
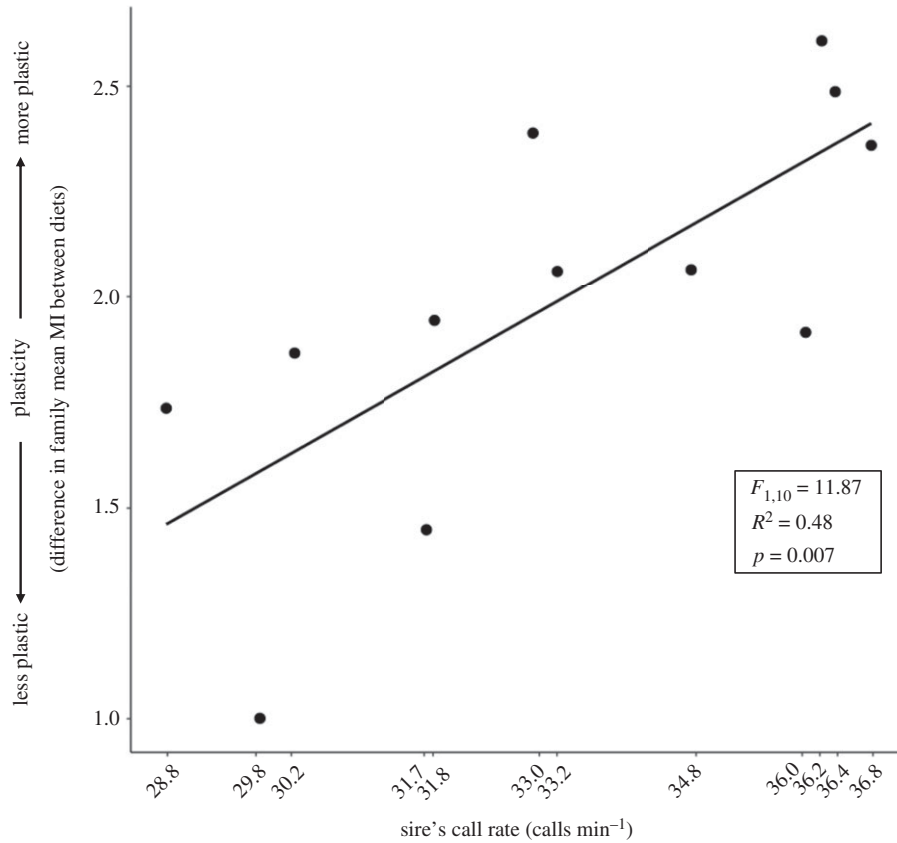
Figure 3. Linear regression of plasticity in resource-use morphology (calculated as differences between family-mean MI values on shrimp versus on detritus diets) on ln call rate (back-transformed).
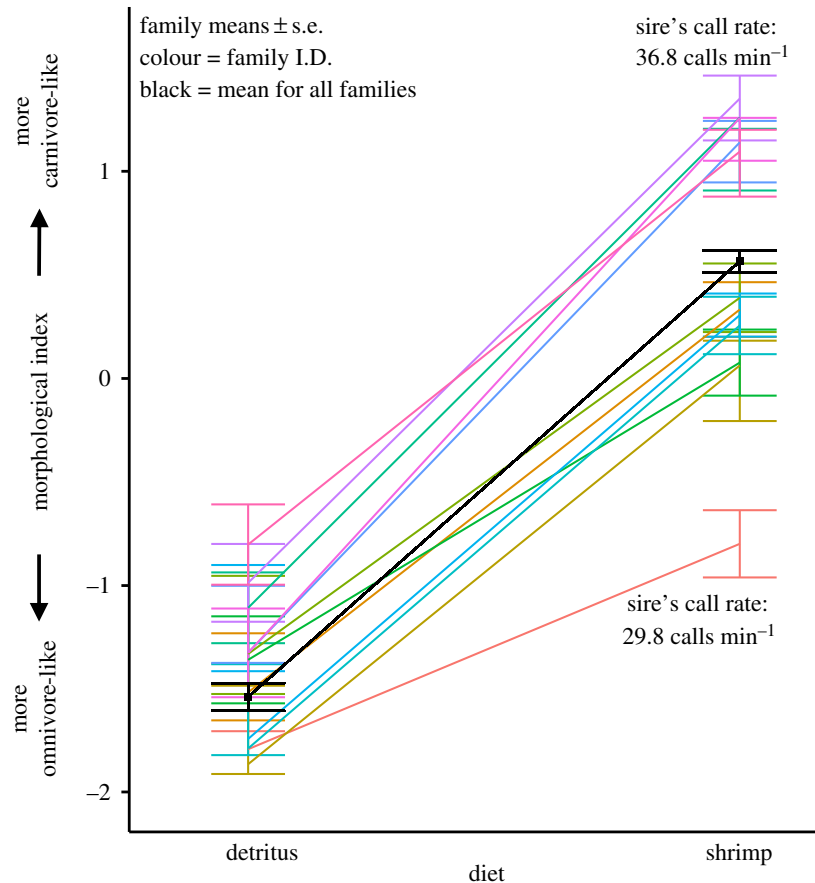
$F_{1,10} = 11.87$
$R^2 = 0.48$
$p = 0.007$

Figure 4. Reaction norms of family-mean morphological index values when tadpoles were reared on detritus versus shrimp diets. Call rates are shown for sires whose tadpoles exhibited the steepest and shallowest reaction norms. (Online version in colour.)

populations studied here, shows that females prefer faster-calling males [46,48]. By doing so, females select males that are generally in better condition and that sire more and larger offspring [46,47]. Our results reveal an additional benefit of choosing faster-calling males: the production of offspring capable of adopting the resource-use morphology best suited for prevailing conditions. In this case, not only did faster-calling males sire more carnivore-like offspring on a shrimp diet (i.e. their offspring produced the resource-use morphology that can best use the shrimp resource [61]), they also produced offspring that displayed greater *plasticity* in resource-use morphology when reared on different diets (shrimp versus detritus). Plasticity could therefore be an indirect 'good genes' benefit that enhances the fitness of a female's offspring (and, indirectly, the female).

The carnivore and omnivore resource-use phenotypes of spadefoots carry different fitness costs and benefits. The nutrient-rich shrimp and tadpole diet of the carnivore phenotype fuels rapid development and, in many cases, an overall larger body size at metamorphosis [50]. Yet, carnivores can face intense competition for resources, especially when prey densities are low and the number (or quality) of competitors is high [54]. Omnivores, by contrast, have lower chances of survival (owing to their slower development and smaller size at metamorphosis), but they face less resource competition and can actually metamorphose in better overall body condition if they have sufficient time to develop [50].

As a consequence of these different costs and benefits, the optimal resource-use morphology that a given tadpole should adopt varies depending on the number of competitor carnivores, the resources available (i.e. the relative abundance of carnivore versus omnivore resources) and the size of the pond (i.e. whether it will dry quickly or more slowly). Each of these factors, in turn, varies both spatially (different ponds can hold more/less water or resources or have different competitor densities) and temporally (rainfall varies year-to-year, as does resource density, which can be tied to pond size) [41,50].

Such a variable environment is expected to favour the evolution of phenotypic plasticity. Indeed, it has long been assumed that plasticity will be favoured when: organisms confront environmental variation; no fixed trait is best suited for all environmental conditions; cues are available that reliably signal a change in local conditions and the fitness benefits outweigh the costs of expressing plasticity [21,69,70]. These conditions apply to spadefoot tadpoles in the variable pond environments described above: neither the omnivore nor the carnivore phenotype is best suited for all conditions [50]; shrimp density and water depth reliably signal resources, competition and pond longevity [49]; and plasticity in resource-use morphology appears to bear relatively few costs compared to the benefits [71]. Thus, plasticity is a trait that is expected to be favoured in this system, and females that prefer males who sire more plastic offspring would likely benefit (by producing more successful offspring) compared to females that lack such preferences. Consequently, female mate choice would promote the evolution of plasticity by generating an added advantage to males who sire more plastic offspring—namely, enhanced mating success.

The possibility that sexual selection—specifically, female choice—might promote the evolution of phenotypic plasticity has not generally been considered. This is especially true for cross-generation or indirect (good genes) effects, whereby females benefit from the production of plastic offspring (figure 1b). Generally, because plastic offspring should have higher fitness than non-plastic offspring in rapidly changing or highly variable environments, females should benefit by preferring males that sire plastic offspring in such environments. Yet, because females are unlikely to be able to directly assess a male's ability to sire plastic offspring, females might generally have to rely instead on male sexual signals that reliably indicate the plasticity of his offspring. If male sexual signals do indeed indicate a male's ability to produce plastic offspring (as we have shown here for spadefoots), and if females prefer such males (as has previously been shown for spadefoots [46,48]), then sexual selection could thereby favour the origin and maintenance of plasticity. Indeed, given the ubiquity of female choice in sexually reproducing species [28,40], female mate choice might play an important and general role in favouring and/or reinforcing the evolution of phenotypic plasticity in many species. Future research on diverse species is needed to ascertain the frequency with which plasticity constitutes a fitness benefit of mate choice, and to clarify female choice's role in the evolution of plasticity.

Conversely, female choice could also explain the evolution of *decreased* plasticity and even the complete *loss* of plasticity. The evolutionary loss of plasticity—'genetic assimilation' (*sensu* [72])—is increasingly viewed as playing a potentially important role in the origins of novel traits and even new species [15,16]. However, researchers have long struggled to explain why selection would ever favour the loss of plasticity [73], unless that plasticity is costly [74]. Yet, few studies have identified such costs of plasticity [75], which deepens the paradox as to why selection would favour the complete loss of plasticity [73]. Our results provide a possible resolution to this paradox: sexual selection as mediated by female mate choice might, under certain circumstances, favour the loss of plasticity. For example, females might be under selection to prefer a more restricted range of male traits (for instance, if they encounter a closely related heterospecific that uses similar sexual signals, as has occurred in certain populations of our focal species [46]), which could simultaneously lead to female choice of males that produce non-plastic offspring. Female choice could thereby promote the loss of plasticity. Likewise, if the benefits of offspring plasticity were concomitantly reduced—for example, if a particular inducible phenotype experienced lower relative fitness, as has also occurred in some populations of our focal system [62]—then females would be under selection to avoid the production of plastic offspring and might evolve preferences for males who produced less (as opposed to more) plastic offspring. In this way, mate choice could also promote an evolutionary loss of plasticity. Either way, sexual selection might be an underappreciated force favouring genetic assimilation. Further studies are needed to address the role of female choice in genetic assimilation.

Sexual selection's interaction with plasticity is not limited to 'good genes' effects in the offspring of males and females. As highlighted in table 1 and §1, plasticity could evolve in the context of male signalling or the expression of female mate choice. If, for example, adults can assess their offspring's environment reliably, selection could favour males that produce different signals of quality in different environments [32,45,76]. Additionally, selection could favour females that facultatively modify their mate preferences so as to optimize their fitness and that of their offspring across different

environments (table 1; [38–40]). Whether selection favours adaptive plasticity at the adult stage (during signalling or mate choice) versus the offspring stage (via 'good genes' effects as seen in this study) will likely depend on the conditions above, and whether adults (as opposed to offspring) are better positioned to assess the cues associated with the production of fitness-enhancing traits in a given environment. Although a growing body of work has revealed how plasticity interacts with sexual selection in generating condition-dependent signals and preferences in adults [40], additional work is needed to evaluate when parents—*as opposed to their offspring*—will evolve plasticity.

Beyond contributing to understanding how sexual selection and plasticity impact each other's evolution, our results also provide insight into the problem of whether sexual selection facilitates or inhibits local adaptation [30,32,33,77,78]. Sexual selection should inhibit local adaptation if patterns of mate choice and male signalling generate a mating advantage for males who sire offspring that are disfavoured in the given environment by natural selection (figure 1*a*). Sexual selection's inhibitory effects on local adaptation are expected to be greatest in variable environments if sexual selection generates evolutionary time lags whereby mate choice and male signals fail to track environmental change (figure 1*a*). Previous work has failed to fully resolve the problem of whether sexual selection can facilitate local adaptation in variable or changing environments [32,78]. Our study suggests that adaptive offspring plasticity represents a solution to this problem. If females preferentially choose males that sire plastic offspring capable of adopting phenotypes best suited for their prevailing environment (figure 1*b*), then sexual selection could facilitate local adaptation even in the most variable and rapidly changing environments.

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