Field and experimental evidence that competition and ecological opportunity promote resource polymorphism

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Resource polymorphism – the occurrence within a single population of discrete intraspecific morphs showing differential resource use – has long been viewed as an important setting for evolutionary innovation and diversification. Yet, relatively few studies have evaluated the ecological factors that favour resource polymorphism. Here, we combine observations of natural populations with a controlled experiment to assess the role of intraspecific competition (specifically, the density of conspecifics) and ecological opportunity (specifically, the range of resources available) on the expression of resource polymorphism in spadefoot toad tadpoles. We found that greater conspecific densities and a greater range of available resources together promoted the expression of resource polymorphism. We conclude that, ecological opportunity, in the form of diverse available resources, along with intraspecific competition, may be a prerequisite for resource polymorphism to evolve, because such polymorphisms require diverse resources onto which each morph can specialize as an adaptive response to minimize competition. © 2010 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2010, **100**, 73–88.

ADDITIONAL KEYWORDS: character displacement – character release – *Spea multiplicata*.

INTRODUCTION

Resource polymorphism – the occurrence within a single population of discrete intraspecific morphs showing differential resource use – rivals speciation as an important source of evolutionary innovation and diversification. Such polymorphisms occur in diverse taxa and they embody some of the most dramatic examples of diversity within species (Smith & Skúlason, 1996; West-Eberhard, 2003). Moreover, resource polymorphisms may represent a critical, early stage in the speciation process (Pfennig & McGee, 2010).

Despite their potential significance, relatively little is known about the conditions that favour the evolution of resource polymorphisms. Generally, such polymorphism is thought to reflect an adaptive response to intraspecific competition for resources (reviewed in Smith & Skúlason, 1996). In a population that exploits a continuously varying resource gradient, intraspecific competition should cause disruptive

selection to favour resource polymorphism, because individuals with extreme resource-use traits specialize on less common, but underutilized, resources (see recent reviews in Bolnick, 2004; Martin & Pfennig, 2009). This process is driven by negative frequency-dependent selection, in which rare resource-use phenotypes have a fitness advantage. In essence, resource polymorphism may be the intraspecific analogue of ecological character displacement; i.e. it may arise through a process of 'intraspecific character displacement' (*sensu* West-Eberhard, 2003).

Resource polymorphism likely requires more than intraspecific resource competition to evolve, however. Although nearly all taxa experience such competition, resource polymorphism is not present in most taxa. As with interspecific character displacement, the evolution of resource polymorphism likely also necessitates ecological opportunity: specifically, the presence of underutilized resources (Pfennig, Rice & Martin, 2006). Because resource polymorphism entails the evolution of a novel resource-use phenotype, underutilized resources must be present for this new phenotype to exploit. In their absence, niche width

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expansion (and, thus, the evolution of resource polymorphism) is not feasible. Such niche width expansion becomes more feasible, however, when underutilized resources are present (Robinson & Wilson, 1994).

The importance of intraspecific competition and ecological opportunity in the evolution of resource polymorphism has proved to be difficult to demonstrate empirically. Some support for the role of competition comes from recent studies showing that intraspecific competition favours extreme trophic phenotypes in natural populations of three-spined stickleback fish (*Gasterosteus aculeatus*, L.) (Bolnick, 2004), Mexican spadefoot toad tadpoles (*Spea multiplicata*, Cope) (Martin & Pfennig, 2009) and Eurasian perch (*Perca flaviatilis*, L.) (Svanbäck & Persson, 2009). Moreover, several studies have shown that competition generates negative frequency dependence among different resource-use phenotypes (Pfennig, 1992; Hori, 1993; Benkman, 1996; Maret & Collins, 1997), which is a hallmark of competitively mediated disruptive selection (Day & Young, 2004). Furthermore, as predicted by theory, resource polymorphisms are found most often in environments where intraspecific competition is severe, underutilized resources are present and interspecific competition is relaxed (the latter two factors combine to increase ecological opportunity) (reviewed in Smith & Skúlason, 1996). Nevertheless, the evidence linking intraspecific competition and ecological opportunity to the evolution of resource polymorphism is incomplete (because ecological opportunity is generally not considered), circumstantial or even contradictory. For example, Olsson, Svanbäck & Eklöv (2006) found that increased intraspecific competition reduced the expression of resource polymorphism in Eurasian perch.

Another consideration is that resource polymorphism is not the only evolutionary response to intraspecific competition (Rueffler *et al.*, 2006). Other possible outcomes include sexual dimorphism (Slatkin, 1984; Bolnick & Doebeli, 2003), behavioural plasticity (Svanbäck & Bolnick, 2007) and character release (especially when functional trade-offs are weak or absent; Taper & Case, 1985). As might be expected, character release (Van Valen, 1965; Robinson & Wilson, 1994; Nosil & Reimchen, 2005; Parent & Crespi, 2009) and sexual dimorphism (Simberloff *et al.*, 2000; Nosil & Reimchen, 2005) are also often found in habitats where intraspecific competition is intense, underutilized resources are present and interspecific competition is relaxed.

Experiments are needed to establish a causal relationship between resource polymorphism on the one hand and intraspecific competition and ecological opportunity on the other. Such experiments are gen-

erally not practical, however, because of the time required to observe an evolutionary response. One way around this problem is to use species in which alternative resource-use morphs arise through phenotypic plasticity. By using these species, one can investigate the conditions that favour the expression of resource polymorphism and infer that these same conditions have likely favoured the evolution of resource polymorphism.

In this study, we undertook such an approach to evaluate the importance of intraspecific competition and ecological opportunity in mediating the expression of resource polymorphism in North American spadefoot toads (genus *Spea*). Four characteristics of *Spea* make them ideal for such investigations. First, *Spea* tadpoles express a striking resource polymorphism, the extremes of which are represented by an 'omnivore' ecomorph, which primarily feeds on organic detritus on the pond bottom, and a 'carnivore' ecomorph, which primarily feeds on anostracan fairy shrimp in the water column (Pomeroy, 1981). Second, different natural populations differ in their degree of expression of this resource polymorphism, as evidenced by variation among populations in the degree of bimodality and variance in trophic morphology (e.g. see Fig. 1). Thus, we could take advantage of this variation to ask what factors predict variation in the degree of expression of resource polymorphism. Third, previous research has revealed that disruptive selection, arising from intraspecific competition for resources, favours these extreme ecomorphs (Martin & Pfennig, 2009). Finally, an individual's trophic phenotype depends largely on its diet, with the most extreme carnivores being induced among individuals that eat the most fairy shrimp (Pfennig, 1990). As noted above, systems in which resource polymorphism arises through such phenotypic plasticity can be used to investigate the conditions that favour the expression of resource polymorphism under the assumption that these same conditions favoured the evolution of the resource polymorphism. Such an assumption underlies many investigations into the selective basis of traits that arise through phenotypic plasticity (West-Eberhard, 2003). Although this assumption may not hold in situations where inducing and selective environments become decoupled (e.g. because of a recent change in the environment), it appears to be valid in the *Spea* system. Specifically, previous studies suggest that the same conditions that induce the alternative morphs also selectively favour these morphs (e.g. see Pfennig & Murphy, 2002).

Using spadefoot toad tadpoles as our model system, we employed observations of natural populations and a controlled experiment to evaluate the importance of intraspecific competition (specifically, the density of
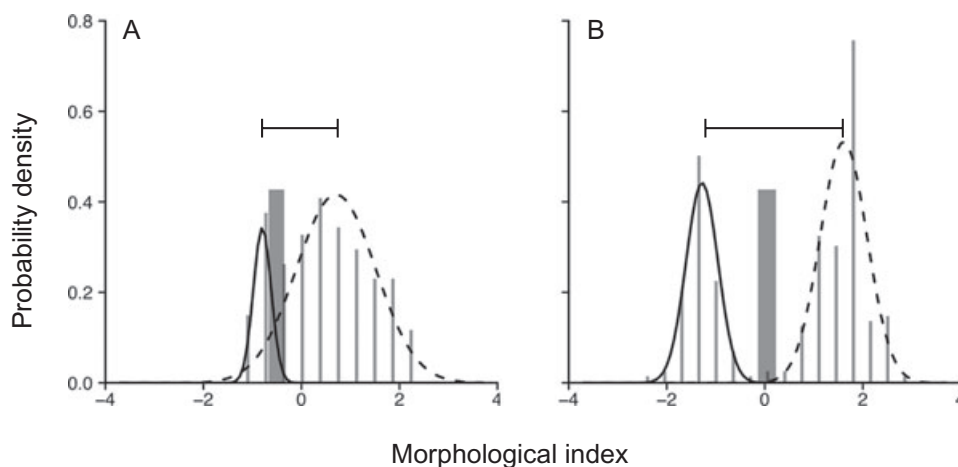
Figure 1. Distributions of tadpole trophic morphology from representative natural pools, showing variation in degree of bimodality and divergence between alternative trophic phenotypes; A, represents pond AZ0603 in Appendix 1. B, represents pond AZ0601 in Appendix 1. Shaded light grey bars represent probability density distributions of tadpole morphological indices, where larger values correspond to tadpoles that are more carnivore-like and smaller values correspond to tadpoles that are more omnivore-like. For both ponds, the solid and dashed curves represent the fitted mixture model for each mode, corresponding to (roughly) omnivores and carnivores, respectively. The single dark grey bars illustrate the window used to estimate the degree of bimodality and which is centred on the intersection of the fitted mixture models. The single, horizontal capped solid lines illustrate the distance between the modes of the fitted mixture models (used to estimate divergence between alternative trophic phenotypes). The distribution for the pond in (A) was weakly bimodal, whereas that for the pond in (B) was strongly bimodal. In addition, the distance between modes in pond (A) was smaller than the distance between modes in pond (B). See Material and methods and Results for details.

conspecifics) and ecological opportunity (specifically, the range of resources available) on the expression of resource polymorphism. To quantify the degree of resource polymorphism, we measured tadpole populations for (1) their degree of bimodality in trophic phenotype (i.e. more discrete trophic phenotypes) and (2) their divergence between trophic phenotypes.

MATERIAL AND METHODS

SURVEYS OF NATURAL PONDS

We collected *S. multiplicata* tadpoles during summers 2006–2009 from 15 natural ponds near Portal, AZ (USA), where *S. multiplicata* was the only *Spea* species present (see Appendix 1). Tadpoles were sampled from randomly selected sites throughout each pond 16–20 days past pond filling by using a hand-held dip net. Immediately after collection, we killed the tadpoles by immersion in a 0.1% aqueous solution of tricane methanesulphonate (MS 222) and preserved them in 95% ethanol. We also used this random sampling technique to estimate the density of *S. multiplicata* tadpoles in each pond as 'high', 'moderate' and 'low' (see also Pfennig, 1990).

We determined the range of available resources in each pond by estimating abundance of fairy shrimp and detritus, the two main resources present in each pond. We estimated fairy shrimp abundance by sweeping a net throughout each pond and categorizing shrimp densities as 'high', 'moderate' and 'low' (these subjective estimates are corroborated by previously published, intensive, quantitative sampling; Pfennig, 1990; Pfennig *et al.*, 2006). We also assessed the availability of detritus by estimating the per cent vegetative cover in a 20-m radius around each pond's circumference and categorized each pond as having either 'high' (67–100% cover), 'moderate' (34–66% cover) or 'low' (0–33% cover) detritus (ponds with more vegetation tend to have more detritus; Pfennig *et al.*, 2006). We then calculated an ecological opportunity score using our estimates of fairy shrimp and detritus abundance. To calculate an ecological opportunity score, we assigned numerical values to our estimates of shrimp and detritus abundance ('high' = 2, 'medium' = 1 and 'low' = 0) and used the formula (shrimp × detritus)/(shrimp + detritus). Therefore, ponds deficient in either shrimp or detritus would be lacking in ecological opportunity and would receive an ecological opportunity score of zero, ponds with intermediate levels of either resource would receive a score between 0 and 1 and ponds with high levels of both shrimp and detritus would receive a score of 1.

We calculated a composite index of each tadpole's trophic morphology following the methods in Pfennig, Rice & Martin (2007). Briefly, we began by measuring

each tadpole's snout–vent length (SVL) using hand-held digital calipers. For each tadpole, we addition-ally measured the width of the orbitohyoideus (OH) muscle and characterized the shape of each tadpole's keratinized mouthparts (MP) on an ordinal scale from 1 (most omnivore-like) to 5 (most carnivore-like). We standardized OH for body size (SVL) by regressing ln (i.e. natural log) OH on ln SVL (all ponds were pooled in a single regression) and used the resulting residu-als for the subsequent analyses (these residuals were distributed normally). We then combined the MP and residuals of ln OH regressed on ln SVL into a single multivariate shape variable (the 'morphological index') by calculating a principal component score. We used PC1, which explained 64% of the variance. By calculating a common morphological index, we could directly compare trophic morphologies among our natural pond collections, where higher values repre-sent individuals that are more carnivore-like and lower values more omnivore-like.

To evaluate the expression of resource polymor-phism in each pond, we first asked whether trophic morphology was distributed unimodally (i.e. com-posed of a single mode) or bimodally (i.e. composed of two modes). To address this issue, we tested whether the distribution of trophic morphology in each pond was better described by a single normal distribution or by a mixture of two normal distributions, using two different methods. First, using maximum likelihood, we fitted a single normal probability density function with a mean and variance corresponding to the numerical mean and standard deviation to the mor-phological index of each pond. We then fitted a two-component mixture model also using maximum likelihood. We seeded each mixture model with start-ing values for each distribution's mean, proportional size and standard deviation. The mean and propor-tional size of each distribution was estimated from visual inspection of the pond's morphological index. A common standard deviation, equal to half of the calculated numeric standard deviation of the pond's morphological index, was used. We evaluated the hypothesis that the mixture of two normal distribu-tions fitted the data better than a single normal distribution using Akaike's information criteria (AIC), corrected for sample size (Burnham & Anderson, 2002). To do so, we calculated ΔAIC_c by taking the difference between AIC_c of the fitted single normal distribution minus AIC_c of the mixture of two normal distributions. Following Burnham & Anderson (2002), we interpreted $\Delta AIC_c > 4$ as more support for the fit of a mixture model than the fit of a single normal distribution, while ΔAIC_c between –4 and 4 as equiva-lent support for the fit of the mixture model and single normal distribution, and ΔAIC_c less than –4 as more support for the fit of a single distribution. In

addition, we used a Bayesian framework to fit the single normal distribution and the mixture of two normal distributions for each pond, using the methods and software describe in Brewer (2003). We did so to corroborate the results of the maximum likelihood method. As above, we used ΔAIC_c to deter-mine the best-fit model.

Because there was strong support for bimodality in 13 of 15 ponds, and equivalent support for unimodal-ity and bimodality in two ponds (Appendix 1), we estimated the degree of bimodality and the divergence between trophic phenotypes in each pond, using the distributions fit using maximum likelihood. We used these measures as an indication of the degree of expression of resource polymorphism in each pond. Our measure of the degree of bimodality was 1 minus the proportion of values falling between the two modes of trophic morphology in each pond. Ponds expressing greater bimodality in trophic morphology should have more discrete modes characterized by having fewer intermediate phenotypes between modes and, consequently, a greater bimodality score. To determine the proportion of values falling between modes in each pond, we numerically solved for the point of intersection between the fitted normal distri-butions of the mixture model for each pond using the formula:

$$x = \frac{1}{\sigma_2^2 - \sigma_1^2}\left((\sigma_2^2 u_1 - \sigma_1^2 u_2) \pm \sigma_1\sigma_2\sqrt{(u_2 - u_1)^2 + 2(\sigma_2^2 - \sigma_1^2)\ln\left(\frac{P_1\sigma_2}{P_2\sigma_1}\right)}\right),$$

where $u_{1,2}$, $\sigma_{1,2}$ and $P_{1,2}$ represent the mean, standard deviation and proportional size, respectively, of the best-fit mixture model for each pond. When the means and standard deviations differ between modes, there will be two points of intersection between the modes. We chose the point of intersection lying between, rather than outside the modes. We then determined the proportion of values within a small window around the intersection between the modes (±0.25 units of the morphological index, see Fig. 1). We chose this specific value to restrict our window to the area between modes and to exclude the modes themselves. Our results were qualitatively similar when slightly smaller or larger windows were used (±0.2). To measure the divergence between trophic phenotypes in each pond we calculated the distance between the modes of the fitted mixture model for each pond (see Fig. 1).

We fit a linear model to evaluate if greater intraspe-cific competition, and ecological opportunity, was associated with greater bimodality in trophic pheno-type. Our measures of intraspecific competition (con-specific density) and ecological opportunity (ecological opportunity score) were treated as fixed effects. The degree of bimodality in each pond was the response.

We also included an interaction between our fixed effects in the model.

Next, we fit a linear model to evaluate if greater intraspecific competition, and greater ecological opportunity, was associated with greater divergence between trophic phenotypes. Our measures of intraspecific competition (conspecific density) and ecological opportunity (ecological opportunity score) were treated as fixed effects. The distance between the modes of the fitted mixture model for each pond was the response measure. We also included an interaction between our fixed effects in the model.

MESOCOSM EXPERIMENT

We designed and carried out an experiment to determine the affects of both intraspecific competition and ecological opportunity on the expression of resource polymorphism. We experimentally manipulated the intensity of intraspecific competition by altering tadpole density. We experimentally manipulated ecological opportunity by altering the availability of one of the two main resource types, while keeping that of the other resource type constant. An important caveat to consider is that our experimental manipulation of ecological opportunity could also affect the intensity of competition, because competition should generally be more intense whenever the supply of resources is low relative to demand.

The experimental design consisted of 24 wading pools (1.5 m diameter × 0.25 m high) placed in an open field at the Southwestern Research Station (SWRS) near Portal, AZ. We assigned each pool to one of two density treatments: (1) a low-conspecific density treatment group (the 'low-competition' treatment) or (2) a high-conspecific density treatment group (the 'high-competition' treatment). We also assigned each pool to one of two ecological opportunity treatments: (1) a poor-detritus availability treatment (the 'low-ecological opportunity' treatment) or (2) a rich-detritus availability treatment (the 'high-ecological opportunity' treatment). We combined these two treatments into a full factorial design with six replicate pools per treatment combination. Treatments were alternated spatially within the array of experimental pools.

We chose to manipulate detritus (rather than shrimp) in our ecological opportunity treatment for two reasons. First, we were concerned that a high-shrimp treatment would induce a high frequency of carnivores, which would result in widespread cannibalism in our wading pools (carnivores are highly cannibalistic; Pomeroy, 1981). Second, by creating rich and poor detritus treatments, our experimental manipulation mimicked natural variation observed among ponds in the Portal area, where some ponds are rich in detritus resources, whereas others (such as 'playa' lakes that form in evaporite basins) lack detritus resources (Pfennig *et al.*, 2006).

We began by providing each pool with soil collected from dry ponds in which *Spea* typically breed. We collected soil from four ponds that we had previously determined were rich in detritus, and from three ponds that we had previously determined were poor in detritus, using tadpole growth as a bioassay (see Pfennig *et al.*, 2006). Soil from the four detritus-rich ponds was mixed thoroughly together, whereas that from the three detritus-poor ponds was mixed thoroughly together. We then spread 13 L of one soil type evenly across the bottom of each pool to a depth of approximately 1 cm. Pools were then filled to a depth of 25 cm with well water.

To obtain experimental subjects for this experiment, we collected 20 amplectant pairs of adult *S. multiplicata* from a pond near Rodeo, NM (approximately 18 km from SWRS). We chose this population for our study subjects because it is one in which *S. multiplicata* co-occurs with *Spea bombifrons* (Cope) and *S. multiplicata* from such sympatric sites produce a reduced frequency of carnivores (as an outcome of ecological character displacement with *S. bombifrons*; Pfennig & Murphy, 2002). Therefore, we anticipated that *S. multiplicata* tadpoles derived from this population would produce a relatively low frequency of carnivores (i.e. a lower frequency than those produced by tadpoles derived from pure *S. multiplicata* populations; see Results), which would reduce the potential for cannibalism (and, hence, mortality).

Adults oviposited in separate plastic aquaria. Two days after their tadpoles hatched, we mixed 17 clutches together in a wading pool and added lettuce for food. Later that day, we randomly chose and distributed these tadpoles into the separate experimental wading pools. We added 1080 tadpoles to each high-competition pool and 180 tadpoles to each low-competition pool. These densities lie within the range of densities found in natural ponds (Pfennig, 1990).

We fed an equal amount of live, wild-caught fairy shrimp to each pool each morning, starting the day the tadpoles were added. We collected fairy shrimp each day with dip nets from two different ponds near Rodeo. We then added fairy shrimp to a bucket filled with 13 L of water and, mixing the bucket between wading pools, added 500 mL of shrimp-saturated water to each pool. These shrimp densities were within the range of shrimp densities found in natural ponds.

We ended the experiment after 12 days. We captured every surviving tadpole from each pool. We killed the tadpoles by immersion in a 0.1% aqueous solution of MS 222 and preserved them in 95% ethanol. To evaluate if the proportion of

carnivores differed between high-competition and low-competition treatments, we visually scored the proportion of carnivore tadpoles in each pond. We used an arcsine-root transformation of the data to fit the assumptions of a parametric test. We then used a linear mixed-effect model, with conspecific density as a fixed effect and arcsine-root transformed proportion of carnivores as the response variable. We included pool ID as a random effect to account for unmeasured variation among pools.

We used every tadpole we collected from the low-competition pools in the following analyses. However, we randomly selected up to 500 tadpoles from each high-competition pool for the analysis. For each wading pool, we combined three trophic characters [MP, OH and the number of labial teeth rows (LT)] into a morphological index as described before.

First, we asked if intraspecific competition disfavoured intermediate trophic phenotypes in our experimental pools and if the strength of disruptive selection differed between experimental treatments. We tested for selection on trophic morphology in each pool using two fitness proxies: Gosner developmental stage (a commonly used guide for staging anuran larvae; see Gosner, 1960) and body size (ln SVL; see Martin & Pfennig, 2009). These likely serve as reliable proxies for fitness: there is a premium on rapid development in the ephemeral ponds in which *S. multiplicata* typically breed (Pfennig, 1992) and larval body size predicts several fitness components (Martin & Pfennig, 2009). We separately regressed each of these fitness proxies onto the morphological index. For this analysis only, the morphological index was calculated separately for each experimental pool. We performed linear and quadratic regressions on the tadpoles from each pool separately. We chose the best regression model for each dataset by comparing the Akaike's information criterion, corrected for sample size (AIC_c), for each model (Burnham & Anderson, 2002). In addition, we performed cubic spline analyses to verify the presence of a fitness minimum (Schluter, 1988). We fit linear mixed-effect models to evaluate whether disruptive selection differed between experimental treatments. We included conspecific density and detritus availability, and the interaction between conspecific density and detritus availability as a fixed effect in our models. Our response measure was the quadratic selection gradient, γ (Lande & Arnold, 1983; Stinchcombe *et al.*, 2008), obtained from our separate regressions of trophic morphology and our two fitness proxies (ln SVL and Gosner stage) in each pool. We included pool ID as a random effect as described before.

Because we found a significant interaction between conspecific density and detritus availability, we then used Tukey's HSD to test for differences between the conspecific density/detritus availability treatment combinations. In addition, because each estimate of the γ has an associated error, not accounted for in the above analyses, we estimated the median values of mean γ, as well as 95% confidence intervals for each of the four treatment combinations using re-sampling. We performed our re-sampling by bootstrapping the individual regressions of body size and Gosner stage from each pool and then calculating a mean γ for each treatment. We used 10 000 bootstrap replicates for each pool to create a pool of 10 000 estimates of the mean γ for each treatment. We then calculated the median of the mean value of γ, as well as the 95% confidence intervals for each treatment combination.

Using the methods previously described (see Surveys of natural ponds above), we next evaluated whether the distribution of trophic morphology in each pool was significantly bimodal. Because there was greater support for bimodality than unimodality in every pool (Appendix 5), we then measured the degree of bimodality and divergence between trophic phenotypes in each pool. We also confirmed that our different sampling procedures for different conspecific-density treatments (in which we sampled all tadpoles from the low-competition pools, but potentially only a subset of tadpoles from the high-competition pools) did not bias our results. To do so, we recalculated the degree of bimodality and divergence between trophic phenotypes in each pool after using reduced sample sizes from each high-competition pool (180 tadpoles; obtained by random sampling without replacement). Because the results obtained from both sampling procedures were qualitatively similar, we report results utilizing the larger sample size.

We fit a linear mixed-effect model to evaluate if intraspecific competition (i.e. conspecific density) and ecological opportunity (i.e. the availability of detritus resources) promote bimodality in trophic morphology. We included conspecific density, detritus availability and their interaction as fixed effects in our model. Our estimate of the degree of bimodality in each pool was the response measure. We included pool ID as a random effect as described before.

Finally, we fit a linear mixed-effect model to determine if conspecific density and detritus availability promote greater divergence between trophic phenotypes. We included conspecific density, resource availability and their interaction as fixed effects in our model. Our response measure was the distance between the modes of the fitted mixture model for each pool. We included pool ID as a random effect as described before. All analyses were carried out in R (2.9.2).

RESULTS

SURVEYS OF NATURAL PONDS

We found strong support for bimodality in 13 of 15 natural ponds and equivalent support for unimodality and bimodality in two ponds (see Appendix 1). Additionally, our estimate of competition (conspecific density) predicted the degree of bimodality ($F_{1,11} = 20.372$, $P = 0.0009$). In particular, ponds with greater conspecific density exhibited greater bimodality (i.e. they produced more discrete trophic phenotypes; Fig. 2A). In contrast, neither ecological opportunity (the range of resources available) nor the interaction between conspecific density and ecological opportunity predicted the degree of bimodality (ecological opportunity: $F_{1,11} = 0.024$, $P = 0.881$; conspecific density × ecological opportunity: $F_{1,11} = 3.003$, $P = 0.111$).

In contrast, both ecological opportunity ($F_{1,11} = 6.748$, $P = 0.025$) and conspecific density ($F_{1,11} = 8.253$, $P = 0.015$) predicted divergence between trophic phenotypes. In particular, ponds with greater ecological opportunity (greater abundances of both fairy shrimp and detritus) expressed greater divergence between trophic phenotypes (Fig. 2B). Similarly, ponds with greater conspecific density also expressed greater divergence between trophic phenotypes (Fig. 2C). However, the interaction between ecological opportunity and conspecific density did not predict divergence between trophic phenotypes ($F_{1,11} = 0.114$, $P = 0.743$).

MESOCOSM EXPERIMENT

We found that disruptive selection disfavoured individuals that were intermediate in trophic morphology. Specifically, a quadratic regression with positive γ significantly fit the data in every pool and was the best-fit model in 23 of 24 pools for body size and 21 of 24 pools for developmental stage (see Appendix 2). In addition, cubic spline analyses verified the presence of a fitness minimum in each pool. We further found that the intensity of disruptive selection was affected by conspecific density (ln SVL: $F_{1,20} = 86.615$, $P < 0.0001$; Gosner stage: $F_{1,20} = 143.695$, $P < 0.0001$), resource availability (ln SVL: $F_{1,20} = 19.863$, $P < 0.0001$; Gosner stage: $F_{1,20} = 35.039$, $P < 0.0001$) and their interaction (ln SVL: $F_{1,20} = 37.955$, $P < 0.0001$; Gosner stage: $F_{1,20} = 11.986$, $P < 0.0001$). Post hoc tests revealed significant differences among the conspecific density/detritus availability treatments (Fig. 3, see also Appendix 3). Furthermore, our estimates of γ for each treatment fall within the range of γs obtained by bootstrap re-sampling (Fig. 3, see also Appendix 4).

The distributions of trophic phenotypes were significantly bimodal in all 24 experimental pools, irre-
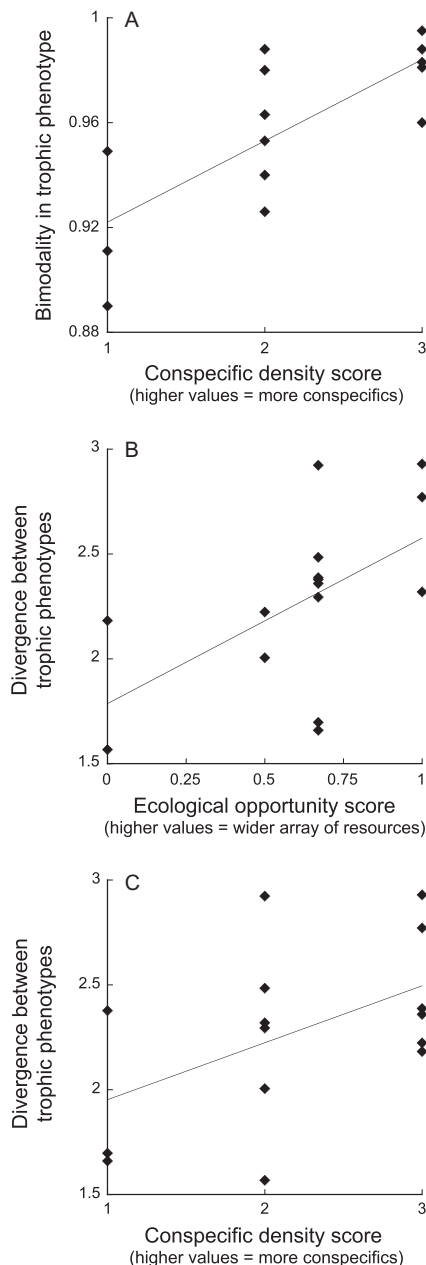

Figure 2. Relationships in natural ponds between intraspecific competition and ecological opportunity on the one hand and the expression of resource polymorphism on the other. A, relationship between conspecific density (a measure of the intensity of intraspecific competition) and degree of bimodality in trophic phenotype. B, relationship between ecological opportunity scores (a composite measure of the range of available resources) and divergence between trophic phenotypes. C, relationship between conspecific density and divergence between trophic phenotypes. See Material and methods and Results for details.
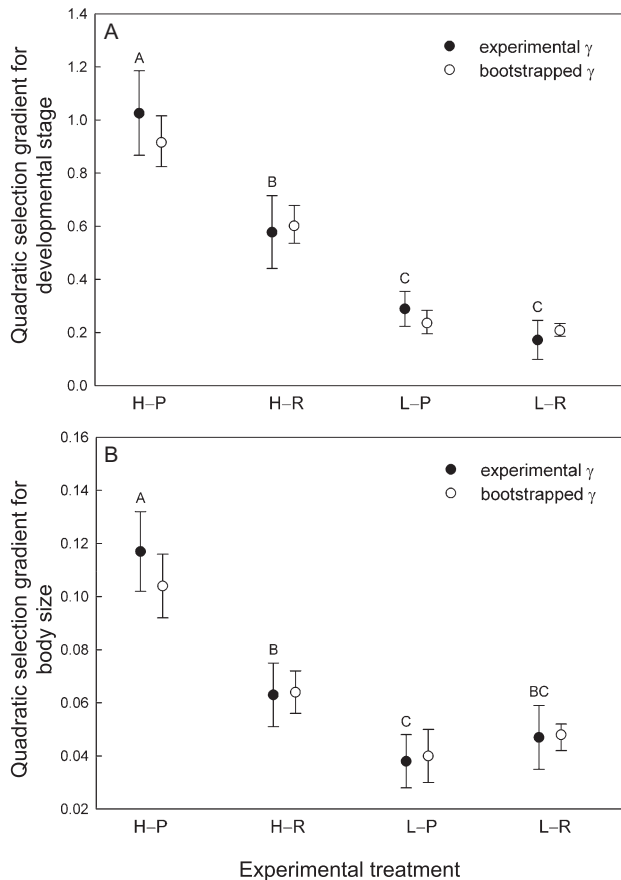
Figure 3. Effect of competition and ecological opportunity on the intensity of disruptive selection on trophic morphology. Developmental (Gosner) stage (A) and body size (B) (ln SVL, mm) serve as fitness proxies. Experimental treatments are H–P: high-conspecific density, poor-detritus availability; H–R: high-conspecific density, rich-detritus availability; L–P: low-conspecific density, poor-detritus availability; and L–R: low-conspecific density, rich-detritus availability. Filled circles and their associated error bars represent the mean quadratic selection gradient (γ) of the six experimental pools in each treatment and the associated standard deviations. Treatment means not sharing an uppercase letter were significantly different from each other. Open circles and their associated error bars represent the median of the mean γ for each treatment estimated from 10 000 bootstrapped quadratic regressions for each pool and the associated 95% confidence intervals. See Material and methods and Results for details.

spective of treatment (see Appendix 5). However, experimental pools in the high-competition treatment exhibited greater bimodality (i.e. they produced more discrete resource-use phenotypes) than pools in the low-competition treatment (high-competition: 0.963 ± 0.012, low-competition: 0.924 ± 0.027, $F_{1,20} = 5.506$, $P = 0.029$; Fig. 4; also see Appendix 5). In contrast,

there was no effect of resource treatment ($F_{1,20} = 0.583$, $P = 0.454$), or the interaction between density and resource treatments ($F_{1,20} = 0.109$, $P = 0.745$), on the degree of bimodality. However, by the end of the experiment, the mean (± SEM) proportion of individuals that were carnivores was actually significantly greater in the low-competition treatment (0.034 ± 0.022) than in the high-competition treatment (0.013 ± 0.001; $F_{1,22} = 16.179$, $P = 0.0006$).

Resource availability affected divergence between trophic phenotypes. Specifically, divergence was greater in the rich-detritus availability treatment (rich-detritus: 3.666 ± 0.6, poor-detritus: 3.065 ± 0.441, $F_{1,20} = 7.297$, $P = 0.0137$, Fig. 4; also see Appendix 5). In contrast, there was no effect of density ($F_{1,20} = 0.341$, $P = 0.566$), or the interaction between density and resource treatments ($F_{1,20} = 0.024$, $P = 0.878$), on divergence between trophic phenotypes.

DISCUSSION

Evolutionary ecologists have long hypothesized that intraspecific competition acts as a potent agent of disruptive selection. According to this theory (reviewed in Bolnick, 2004; Martin & Pfennig, 2009), individuals that specialize in less common, but underutilized, resources on either end of a resource gradient will have a fitness advantage. Over time, this selection can favour alternative resource-use morphs within the same population; i.e. a resource polymorphism. Although longstanding, this theory has been subjected to few experimental tests. Moreover, such tests often fail to consider the importance of ecological opportunity. Generally, a resource polymorphism should only evolve when intraspecific resource competition is intense and ecological opportunity is high; i.e. when the resource gradient is wide enough to allow each morph in a resource polymorphism to specialize on an alternative resource. In this study, we used spadefoot toad tadpoles to test this general hypothesis.

Our results demonstrate that both intraspecific competition and ecological opportunity promote the expression of resource polymorphism and therefore suggest that they are necessary for the evolution of resource polymorphism. Specifically, four lines of evidence indicate that intraspecific competition promotes resource polymorphism. First, natural ponds with the greatest density of conspecifics (a measure of the intensity of competition) expressed the most bimodal (i.e. the most discrete) distributions of trophic phenotypes (Fig. 2A). Second, natural ponds with the greatest density of conspecifics (a measure of the intensity of competition) expressed the greatest divergence between trophic phenotypes (Fig. 2C). Third, selection against intermediate phenotypes in our mesocosm
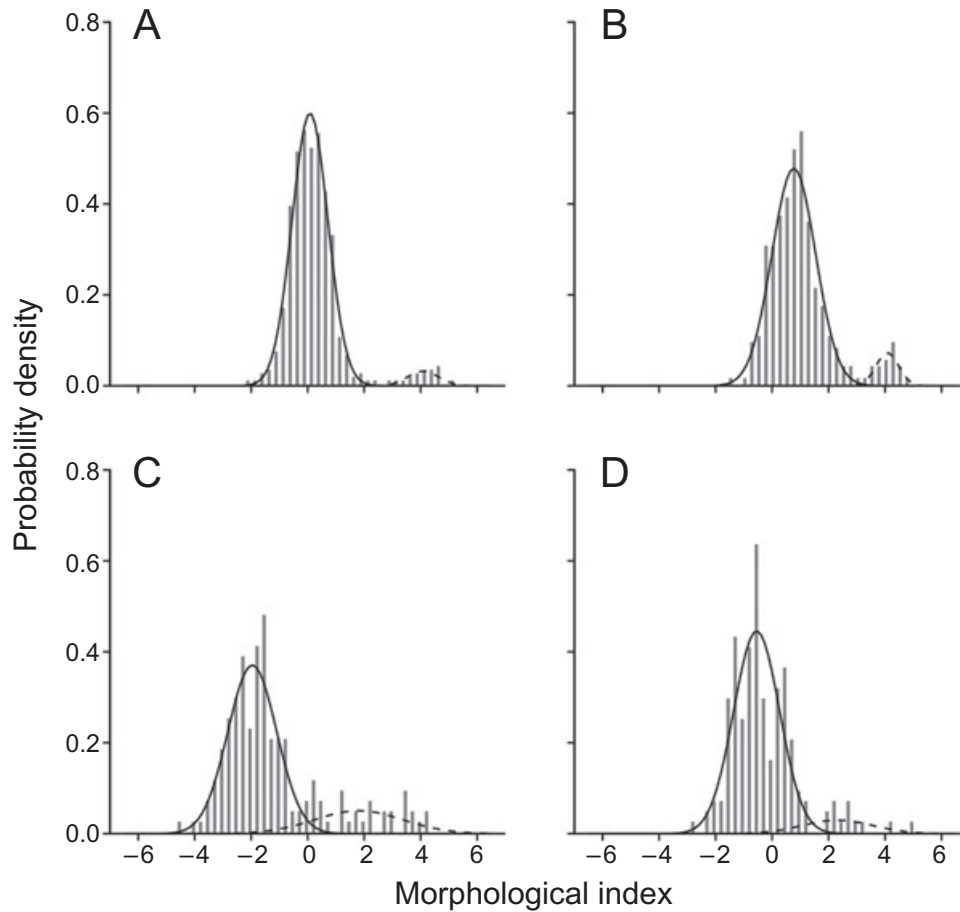
Figure 4. Distributions of tadpole trophic morphology from representative experimental pools, including (A) a high-conspecific density, rich-detritus availability pool, pool 5, (B) a high-conspecific density, poor-detritus availability pool, pool 12, (C) a low-conspecific density, rich-detritus availability pool, pool 17 and (D) a low-conspecific density, poor-detritus availability pool, pool 20 (see Appendix 5). Shaded grey bars represent probability density distributions of tadpole morphological indices, where larger values correspond to tadpoles that are more carnivore-like and smaller values correspond to tadpoles that are more omnivore-like. The solid and dashed curves represent the fitted mixture model for each mode, corresponding to (roughly) omnivores and carnivores, respectively. See Material and methods and Results for details.

experiment tended to be more intense in the high than in the low-competition treatments (Fig. 3; Appendix 3; see also Bolnick, 2004; Martin & Pfennig, 2009). Fourth, in our mesocosm experiment, tadpoles produced greater bimodality in trophic phenotype in the high-competition treatment than in the low-competition treatment (e.g. Fig. 4). These results, together with those of a previous study (Martin & Pfennig, 2009), demonstrate that intraspecific competition favours extreme resource-use morphs.

Two lines of evidence support the prediction that ecological opportunity is also critical for the evolution of niche-width expansion and therefore resource polymorphism. First, natural ponds with the greater availability of fairy shrimp and detritus resources (a measure of ecological opportunity) expressed greater divergence between trophic phenotypes (Fig. 2B). Second, in our mesocosm experiment, the greatest divergence between trophic phenotypes was expressed in rich-detritus availability pools (e.g. Fig. 4A, C).

As further evidence that both intraspecific competition and ecological opportunity are essential for the expression (and, presumably, the evolution) of resource polymorphism, we found that bimodality and divergence between trophic phenotypes (and thus, the expression of resource polymorphism) was greatest in our mesocosm experiment where both competition and resource availability were greatest (Fig. 4A). The finding that disruptive selection was greatest in pools where conspecific density was greatest and the range of resources was decreased (Fig. 3) strongly suggests

that the increased range of resources in the rich-resource, high-competition treatment allowed the experimental populations to expand the range of resources used as an adaptive response to lessen competition, as predicted by theory.

We observed cannibalism in our wading pools, which raises an important question: did the greater bimodality in high-competition pools (e.g. Fig. 4A, B) arise merely as a consequence of more carnivores being produced in response to an increased abundance of conspecific prey? Although shrimp ingestion is the more important environmental cue for inducing carnivores (Pomeroy, 1981; Pfennig, 1990), cannibalism can also induce carnivores (Pomeroy, 1981). Thus, it might be contended that the positive relationship between tadpole density and degree of bimodality arose, not as an adaptive response to lessen competition for food, but as a response to an increase in prey for cannibalistic individuals to eat. Two lines of evidence argue against this alternative hypothesis, however. First, in our experimental pools, individuals that were intermediate in trophic morphology were smaller and less developed (see Results) than were either omnivores or carnivores. The reduced size and development of intermediates can be explained readily by competition (Martin & Pfennig, 2009), but not by predation (carnivores preferentially target omnivores, not intermediates, as prey; D.W. Pfennig, pers. observ.). Second, contrary to the predictions of the predation hypothesis, a higher frequency of carnivores was actually produced in low-conspecific-density pools than in high-conspecific-density pools (see Results). Thus, our data are most consistent with the hypothesis that bimodality in trophic phenotype arose primarily as an adaptive response to lessen intraspecific competition for food.

Although we used conspecific density as our proxy for the intensity of intraspecific competition, competition should generally be more intense whenever the supply of resources is low relative to demand. This relationship should hold regardless of whether the demand (e.g. conspecific density) is high or whether the supply (e.g. the range of resources available) is low. Yet, in our mesocosm experiment, we found no effect of resource treatment (i.e. supply) on the degree of bimodality (see Results). One possible explanation for this result is that the increase in bimodality may arise as an adaptive response to interference competition, in which individuals directly impede the foraging of others, rather than to exploitative competition, which occurs indirectly through the consumption of a shared, limited resource. A decrease in the range of resources available should have intensified only exploitative competition, but an increase in the density of conspecifics should have intensified both exploitative and interference competition. The fact that a decrease in the range of resources available did not cause greater bimodality, whereas an increase in the density of conspecifics did, suggests that bimodality may not have resulted purely from exploitative competition, as is often assumed. Generally, the relative contributions of exploitative vs. interference competition to the evolution of resource polymorphism are largely unknown (but see Svanbäck & Persson, 2004; Andersson et al., 2007).

Taken together, our results provide experimental support for the observation that alternative resource-use morphs occur most commonly where intraspecific competition is intense, exploitable resources are present and interspecific competition is relaxed. For example, many lakes in recently glaciated regions of the northern hemisphere are relatively species poor, which serves to increase ecological opportunity. Moreover, resources are often limited, which tends to increase intraspecific competition. In such lakes, many species of fish express sympatric benthic and limnetic ecomorphs, which specialize in macroinvertebrates in the littoral zone or plankton in the open water, respectively (reviewed in Robinson & Wilson, 1994). Similarly, alternative resource-use morphs in larval amphibians are found in species-poor habitats where intraspecific competition is intense (Pfennig, 1990; Walls, Belanger & Blaustein, 1993; Michimae & Wakahara, 2002).

In conclusion, our study suggests that resource polymorphism does indeed evolve as an adaptive response to lessen intraspecific competition for resources. However, our results also suggest that resource polymorphisms are more likely to evolve when ecological opportunity is present. Because resource polymorphism might represent a critical, early stage in the speciation process (Smith & Skúlason, 1996; West-Eberhard, 2003; Pfennig & McGee, 2010), research into the conditions that favour resource polymorphism might also help clarify the conditions that initiate species formation.

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APPENDIX 1

Estimates of conspecific density, ecological opportunity and the expression of resource polymorphism in natural ponds. Divergence and bimodality are measures of resource polymorphism. Divergence is a measure of the distance between modes of the fitted maximum likelihood mixture models for each pond. Our degree of bimodality was 1 minus the proportion of values falling between the two modes of trophic morphology, fitted by maximum likelihood, in each pond. Conspecific density score is an estimate of competition, shrimp density, detritus density and % vegetation are measures of resource availability. Ecological opportunity score is a composite score of the amount of ecological opportunity. Greater expression of resource polymorphism is indicated by greater divergence and larger values of bimodality. ML ΔAIC_c is the difference between the single normal distribution and the mixture of two normal distributions fitted using maximum likelihood. B ΔAIC_c is the difference between the single normal distribution and the mixture of two normal distributions fitted using Bayesian methods. $\Delta AIC_c > 4$ suggest more support for the fit of a mixture model than the fit of a single normal distribution, while ΔAIC_c between -4 and 4 suggest equivalent support for the fit of the mixture models and single normal distribution and ΔAIC_c below -4 suggest more support for the fit of a single normal distribution.

Pond	Sample size	Conspecific density	Shrimp density	% vegetation	Detritus availability	Ecological opportunity score	Divergence	Bimodality	ML ΔAIC_c	B ΔAIC_c
AZ0601	258	2	2	1	2	1	2.771	0.988	288	303
AZ0602	134	1	2	0.8	2	1	2.319	0.940	24	32
AZ0603	124	0	1	0.75	2	0.66	2.378	0.911	31	27
AZ0604	84	1	2	0.5	1	0.66	2.484	0.988	41	44
AZ0605	176	2	1	0.6	1	0.5	2.223	0.983	86	86
AZ0607†	102	1	0	0.4	1	0	1.568	0.980	−4	7
NM0608	157	2	1	1	2	0.66	2.387	0.981	79	80
AZ0706†	167	0	1	0.7	2	0.66	1.697	0.890	11	1
AZ0710	102	2	0	0.9	2	0	2.182	0.960	35	36
AZ0801	99	0	1	1	2	0.66	1.660	0.949	10	17
AZ0802	150	1	1	0.7	2	0.66	2.294	0.953	99	92
AZ0810	213	2	1	0.8	2	0.66	2.359	0.981	150	152
AZ0812	188	1	1	0.6	1	0.66	2.923	0.963	82	84
AZ0813	135	1	1	1	2	0.5	2.005	0.926	13	12
AZ0902	211	2	2	1	2	1	2.929	0.995	338	331

†Equivalent support for bimodality and unimodality.

APPENDIX 2

The mode and strength of selection on trophic morphology in experimental pools. Density treatments are represented by H (high-conspecific density) and L (low-conspecific density). Resource treatments are represented by R (rich-detritus availability) and P (poor-detritus availability). PC1 is a composite shape variable that measures trophic morphology. The fitness measures, sample size and regression terms are given for each pool, along with the estimated selection gradient for each term, its standard error (SE), t-statistic, probability of rejecting the null hypothesis that the estimated coefficient is zero and the Akaike's information criterion corrected for sample size (AIC_c). For quadratic regressions, positive selection gradients signify disruptive selection and the quadratic regression coefficient is doubled to calculate the quadratic selection gradient (γ) and the associated standard error (SE) is also doubled. Bolding signify models with the best fit (i.e. the model with the lowest AIC_c value).

Pool	Density treatment	Resource treatment	Fitness measure	Regression term	Selection gradient (β/γ)	SE/2SE	t	P	AIC_c
1	H	R	ln SVL	PC1	0.065	0.007	10.09	< 0.0001	−293
				PC1^2	0.042	0.0026	15.48	< 0.0001	**−396**
			Development	PC1	0.784	0.108	7.257	< 0.0001	2498
				PC1^2	0.362	0.216	8.898	< 0.0001	**2474**
2	H	R	ln SVL	PC1	0.059	0.007	8.098	< 0.0001	−235
				PC1^2	0.066	0.004	17.06	< 0.0001	**−403**
			Development	PC1	0.752	0.009	8.368	< 0.0001	2265
				PC1^2	0.612	0.054	11.38	< 0.0001	**2216**
3	H	R	ln SVL	PC1	0.064	0.008	7.03	< 0.0001	−108
				PC1^2	0.076	0.004	15.93	< 0.0001	**−258**
			Development	PC1	0.727	0.083	8.66	< 0.0001	2192
				PC1^2	0.724	0.05	14.41	< 0.0001	**2088**
4	H	R	ln SVL	PC1	0.094	0.008	11.2	< 0.0001	−68
				PC1^2	0.058	0.004	16.05	< 0.0001	**−164**
			Development	PC1	0.912	0.088	10.39	< 0.0001	2266
				PC1^2	0.516	0.038	13.27	< 0.0001	**2212**
5	H	R	ln SVL	PC1	0.059	0.009	6.597	< 0.0001	−51
				PC1^2	0.076	0.004	15.74	< 0.0001	**−206**
			Development	PC1	0.582	0.09	6.459	< 0.0001	2317
				PC1^2	0.722	0.054	13.21	< 0.0001	**2207**
6	H	R	ln SVL	PC1	0.049	0.008	6.362	< 0.0001	−149
				PC1^2	0.058	0.004	15.81	< 0.0001	**−308**
			Development	PC1	0.483	0.076	6.328	< 0.0001	2114
				PC1^2	0.534	0.038	13.88	< 0.0001	**1990**
7	H	P	ln SVL	PC1	0.065	0.013	4.927	< 0.0001	95
				PC1^2	0.136	0.01	13.22	< 0.0001	**−22**
			Development	PC1	0.954	0.111	8.611	< 0.0001	1475
				PC1^2	1.296	0.09	14.46	< 0.0001	**1380**
8	H	P	ln SVL	PC1	0.056	0.015	3.832	0.0001	71
				PC1^2	0.12	0.014	9.254	< 0.0001	**12**
			Development	PC1	0.378	0.16	2.369	0.0186	1214
				PC1^2	0.96	0.15	6.405	< 0.0001	**1181**
9	H	P	ln SVL	PC1	0.048	0.012	3.94	< 0.0001	81
				PC1^2	0.11	0.01	12.3	< 0.0001	**−29**
			Development	PC1	0.438	0.144	3.036	< 0.0001	1707
				PC1^2	1.022	10.13	9.035	< 0.0001	**1643**
10	H	P	ln SVL	PC1	0.1	0.016	6.573	< 0.0001	70
				PC1^2	0.104	0.012	8.399	< 0.0001	**49**
			Development	PC1	0.86	0.164	5.329	< 0.0001	1013
				PC1^2	0.896	0.132	6.828	< 0.0001	**997**
11	H	P	ln SVL	PC1	0.063	0.014	4.558	< 0.0001	90
				PC1^2	0.102	0.012	9.409	< 0.0001	**32**
			Development	PC1	0.529	0.138	3.839	0.0002	1454
				PC1^2	0.864	0.112	7.687	< 0.0001	**1415**

APPENDIX 2 *Continued*

Pool	Density treatment	Resource treatment	Fitness measure	Regression term	Selection gradient (β/γ)	SE/2SE	t	P	AIC$_c$
12	H	P	ln SVL	PC1	0.063	0.013	4.711	< 0.0001	105
				PC1^2	0.128	0.012	10.86	< 0.0001	**26**
			Development	PC1	0.52	0.124	4.181	< 0.0001	1455
				PC1^2	1.116	0.11	10.07	< 0.0001	**1385**
13	L	R	ln SVL	PC1	0.029	0.009	2.943	0.004	−146
				PC1^2	0.04	0.006	5.848	< 0.0001	**−168**
			Development	PC1	0.084	0.092	.912	0.364	465
				PC1^2	0.044	0.076	.577	0.565	465
14	L	R	ln SVL	PC1	0.065	0.008	7.929	< 0.0001	−199
				PC1^2	0.07	0.006	10.93	< 0.0001	**−236**
			Development	PC1	0.224	0.072	3.104	0.002	536
				PC1^2	0.193	0.028	6.857	< 0.0001	**504**
15	L	R	ln SVL	PC1	0.041	0.009	4.748	< 0.0001	−214
				PC1^2	0.044	0.008	5.731	< 0.0001	**−223**
			Development	PC1	0.125	0.087	1.447	0.15	629
				PC1^2	0.21	0.08	2.623	0.009	**624**
16	L	R	ln SVL	PC1	0.035	0.007	4.836	< 0.0001	−204
				PC1^2	0.032	0.004	8.44	< 0.0001	**−243**
			Development	PC1	0.079	0.072	1.055	0.293	623
				PC1^2	0.158	0.042	3.731	0.0003	**610**
17	L	R	ln SVL	PC1	0.058	0.006	8.911	< 0.0001	−299
				PC1^2	0.052	0.004	11.04	< 0.0001	**−326**
			Development	PC1	0.291	0.041	7.029	< 0.0001	403
				PC1^2	0.266	0.038	7.004	< 0.0001	403
18	L	R	ln SVL	PC1	0.037	0.011	0.465	0.0007	−80
				PC1^2	0.042	0.08	5.65	< 0.0001	**−98**
			Development	PC1	0.162	0.091	1.772	0.0786	507
				PC1^2	0.16	0.066	2.406	0.0175	**504**
19	L	P	ln SVL	PC1	0.043	0.009	4.657	< 0.0001	−186
				PC1^2	0.042	0.006	6.092	< 0.0001	**−199**
			Development	PC1	0.114	0.114	2.778	0.006	714
				PC1^2	0.266	0.088	3.049	0.003	**713**
20	L	P	ln SVL	PC1	0.053	0.008	6.952	< 0.0001	**−235**
				PC1^2	0.038	0.006	6.211	< 0.0001	−227
			Development	PC1	0.358	0.088	4.052	< 0.0001	**630**
				PC1^2	0.266	0.068	3.872	0.0002	631
21	L	P	ln SVL	PC1	0.033	0.008	4.281	< 0.0001	−213
				PC1^2	0.046	0.01	4.66	< 0.0001	**−216**
			Development	PC1	0.171	0.117	1.464	0.145	741
				PC1^2	0.414	0.154	2.702	0.008	**736**
22	L	P	ln SVL	PC1	0.057	0.011	5.279	< 0.0001	−131
				PC1^2	0.048	0.008	6.146	< 0.0001	**−139**
			Development	PC1	0.365	0.125	2.916	0.004	711
				PC1^2	0.296	0.874	3.454	0.001	**709**
23	L	P	ln SVL	PC1	0.033	0.01	3.338	0.001	−117
				PC1^2	0.032	0.006	4.765	< 0.0001	**−128**
			Development	PC1	0.21	0.119	1.77	0.0785	716
				PC1^2	0.226	0.08	2.818	0.005	**712**
24	L	P	ln SVL	PC1	0.03	0.009	3.201	0.00166	−136
				PC1^2	0.022	0.006	4.193	< 0.0001	**−143**
			Development	PC1	0.449	0.17	2.651	0.00884	802
				PC1^2	0.266	0.1	2.634	0.009	802

APPENDIX 3

Statistical comparison of treatment means of γ using Tukey's HSD. Gosner stage and ln SVL serve as fitness proxies. Treatment combinations are represented by H/P (high-conspecific density; poor-detritus availability), H/R (high-conspecific density; rich-detritus availability), L/P (low-conspecific density; poor-detritus availability), L/R (low-conspecific density; rich-detritus availability). Also given is the mean difference between each comparison, its standard error (SE), z value and probability of rejecting the null hypothesis that treatment means do not differ.

Linear contrasts	Difference	SE	z value	P
Gosner stage				
H/P–H/R	0.447	0.067	6.634	< 0.0001
H/P–L/P	0.737	0.067	10.924	< 0.0001
H/P–L/R	0.854	0.067	12.662	< 0.0001
H/R–L/P	0.289	0.067	4.291	0.0001
H/R–L/R	0.407	0.067	6.028	< 0.0001
L/P–L/R	−0.117	0.067	−1.738	0.304
ln SVL				
H/P–H/R	0.054	0.007	7.508	< 0.001
H/P–L/P	0.079	0.007	10.937	< 0.001
H/P–L/R	0.070	0.007	9.732	< 0.001
H/R–L/P	0.025	0.007	3.429	0.003
H/R–L/R	0.016	0.007	2.225	0.117
L/P–L/R	0.009	0.007	−1.205	0.624

APPENDIX 4

Effect of competition and ecological opportunity on the intensity of disruptive selection on trophic morphology. Experimental treatments are HP (high-conspecfic density; poor-detritus availability), HR (high-conspecific density; rich-detritus availability), LP (low-conspecific density; poor-detritus availability) and LR (low-conspecific density; rich-detritus availability). (a) Development (Gosner stage) and (b) body size (ln SVL, mm) serve as proxies for fitness. Shown are mean quadratic selection gradients (γ) of the six experimental pools in each treatment and the associated standard deviations (SD), the median of the mean bootstrapped γ of each treatment ($\gamma_{bootstrap}$) estimated from 10 000 bootstrapped quadratic regressions for each pool and the associated 95% confidence intervals (CI).

Density/resource treatment	γ (mean)	γ (SD)	$\gamma_{bootstrapped\ mean}$ (median)	$\gamma_{bootstrapped\ mean}$ (upper 95% CI)	$\gamma_{bootstrapped\ mean}$ (lower 95% CI)
Gosner stage					
H/P	1.026	0.159	0.916	1.016	0.824
H/R	0.578	0.137	0.602	0.678	0.536
L/P	0.289	0.066	0.236	0.284	0.195
L/R	0.172	0.074	0.208	0.234	0.185
ln SVL					
H/P	0.117	0.015	0.104	0.116	0.092
H/R	0.063	0.012	0.064	0.072	0.056
L/P	0.038	0.010	0.040	0.050	0.030
L/R	0.047	0.012	0.048	0.052	0.042

APPENDIX 5

Tests for the effect of intraspecific competition and resource availability on the expression of resource polymorphism in experimental pools. Divergence and bimodality are measures of resource polymorphism in each experimental pool. Divergence is a measure of the distance between modes of the fitted maximum likelihood mixture models for each experimental pool. Our degree of bimodality was 1 minus the proportion of values falling between the two modes of trophic morphology, fitted by maximum likelihood, in each experimental pool. Greater expression of resource polymorphism is indicated by greater divergence in trophic phenotype and larger values of bimodality. ML ΔAIC_c is the difference between the single normal distribution and the mixture of two normal distributions fitted using maximum likelihood. B ΔAIC_c is the difference between the single normal distribution and the mixture of two normal distributions fitted using Bayesian mthods. $\Delta AIC_c > 4$ suggest more support for the fit of a mixture model than the fit of a single normal distribution, while ΔAIC_c between −4 and 4 indicate equivalent support for the fit of the mixture models and single normal distribution and values of ΔAIC_c below −4 suggest more support for the fit of a single distribution.

Pool	Survival (%)	Sample size	Density/resource treatment	Divergence	Bimodality	ML ΔAIC_c	B ΔAIC_c
1	0.745	500	H/R	3.063	0.976	369	336
2	0.747	498	H/R	3.949	0.994	268	265
3	0.629	498	H/R	3.636	0.998	280	291
4	0.632	500	H/R	3.732	0.99	385	371
5	0.633	500	H/R	3.969	0.998	311	313
6	0.774	494	H/R	4.138	1	212	213
7	0.31	324	H/P	3.872	1	172	179
8	0.221	239	H/P	2.959	0.983	96	99
9	0.306	330	H/P	2.887	0.97	172	166
10	0.186	201	H/P	2.84	0.965	109	111
11	0.275	296	H/P	2.782	0.99	133	134
12	0.28	302	H/P	3.335	0.99	105	106
13	0.722	130	L/R	4.031	0.98	59	80
14	0.939	169	L/R	4.880	0.994	109	137
15	1	180	L/R	2.695	0.955	196	180
16	0.983	177	L/R	3.086	0.947	70	94
17	0.978	176	L/R	3.642	0.96	78	116
18	0.783	138	L/R	3.165	0.978	53	77
19	0.994	179	L/P	3.591	0.978	160	152
20	0.983	177	L/P	2.787	0.983	37	41
21	0.733	132	L/P	3.254	0.977	72	72
22	0.956	172	L/P	2.869	0.965	52	52
23	0.928	166	L/P	3.382	0.994	37	38
24	0.894	161	L/P	2.219	0.894	108	97