



# Increased competition as a cost of specialization during the evolution of resource polymorphism

JEFFREY S. PAULL, RYAN A. MARTIN† and DAVID W. PFENNIG\*

*Department of Biology, CB #3280, Coker Hall, University of North Carolina, Chapel Hill, NC 27599-3280 USA*

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Identifying the factors that promote or preclude the evolution of resource polymorphism is essential for understanding the origins of diversity. Although such polymorphisms have long been viewed as an adaptive response to intraspecific competition, they are by no means ubiquitous, even in populations experiencing strong competition. In the present study, we examined a potentially important cost of resource polymorphism. Specifically, resource polymorphism typically entails the evolution of one or more resource-use specialists, and these specialists may suffer more from competition with other specialists than generalists would with other generalists. Using spadefoot toad tadpoles as a model system, we combined stable isotope analyses with an experiment aiming to characterize dietary differences between alternative carnivore and omnivore morphs and to assess the potential ecological consequences of any such differences. We found that carnivores and omnivores represent alternative trophic specialists and generalists, respectively. We also established that the specialist morph (carnivores) experienced greater intramorph competition than the generalist morph (omnivores). We hypothesize that the greater intramorph competition faced by specialists stems ultimately from functional limitations associated with trophic specialization, which prevent specialists from switching to alternative resources when their resource is depleted. These costs may even preclude the evolution of distinct resource-use specialists, and hence resource polymorphism, in certain populations. © 2012 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2012, **107**, 845–853.

**ADDITIONAL KEYWORDS:** functional constraints – intraspecific variation – stable isotopes – trade-offs – trophic morphology.

## INTRODUCTION

Resource polymorphisms (i.e. the occurrence within a population of alternative morphs showing differential resource use) are striking examples of intraspecific diversity (Smith & Skúlason, 1996). Indeed, the phenotypic differences between such alternatives often resemble (in kind, if not in degree) the phenotypic differences between distinct species, suggesting that these phenotypic alternatives may represent incipient species (Liem & Kaufman, 1984; Meyer, 1987; West-Eberhard, 1989; Wimberger, 1994; Skúlason, Snorrason & Jónsson, 1999; Adams & Huntingford, 2004; Calsbeek, Smith & Bardeleben, 2007; Wund *et al.*, 2012). Moreover, alternative resource-use morphs may

function ecologically as separate species (Harmon *et al.*, 2009), and their presence might even increase the likelihood that interacting species will coexist (Clark, 2010). Thus, identifying the factors that promote or preclude the evolution of resource polymorphism is crucial for explaining the origin and maintenance of biodiversity.

Resource polymorphism is assumed to evolve as an adaptive response to intraspecific competition (Smith & Skúlason, 1996; Svanbäck *et al.*, 2008; Pfennig & Pfennig, 2012). Longstanding theory predicts that, in a population facing intense intraspecific competition, frequency-dependent disruptive selection should favour alternative resource-use morphs (Doebeli, 2011). Empirical data largely support this prediction (Smith, 1993; Robinson, Wilson & Shea, 1996; Bolnick, 2004; Svanbäck *et al.*, 2008; Calsbeek, 2009; Hendry *et al.*, 2009; Martin & Pfennig, 2009; Cucherousset *et al.*, 2011). Yet, although intraspecific

\*Corresponding author. E-mail: dpfennig@unc.edu

†Current address: Department of Biology, North Carolina State University, Raleigh, NC, USA.

competition is widespread and frequently strong (Gurevitch *et al.*, 1992), resource polymorphism is far from ubiquitous (Smith & Skúlason, 1996). Thus, there may be fitness costs of resource polymorphism that can preclude its evolution.

Consider that resource polymorphism typically entails the evolution of one or more resource-use specialists (Liem & Kaufman, 1984; Hori, 1993; Smith, 1993; Benkman, 1996; Robinson & Wilson, 1998). Although ecological specialization carries benefits, it also potentially carries costs (Futuyma & Moreno, 1988; Dennis *et al.*, 2011). For example, by evolving traits that allows it to specialize on a particular set of resources, an organism may be limited in its ability to harvest alternative resources. Such functional trade-offs may be especially likely to arise if different morphological, physiological, and/or cognitive attributes are required to harvest alternative resources (Benkman, 1996; Robinson *et al.*, 1996; Bolnick *et al.*, 2003; Martin & Pfennig, 2009; Ellerby & Gerry, 2011). Consequently, compared to generalists in the same population, resource-use specialists may have lower fitness if they are forced to switch to another resource for which they are poorly adapted (as might occur, for instance, if their original resource is in short supply or if it is depleted).

Moreover, as their resources became scarce, specialists would likely suffer an additional cost: increased competition with other specialists. Indeed, although the evolution of a resource polymorphism may reduce overall resource competition, the individual resource-use specialists that constitute the resource polymorphism may experience greater 'intramorph' competition than would the ancestral, nonpolymorphic generalists. In some cases, this competition might be so severe that it precludes the evolution of the resource polymorphism.

We aimed to detect these costs in natural populations of an amphibian. Many populations of Mexican spadefoot toads (*Spea multiplicata*, Cope) contain an 'omnivore' morph and a morphologically and behaviourally distinctive 'carnivore' morph (Martin & Pfennig, 2009; Ledón-Rettig & Pfennig, 2011). Pomeroy (1981) found that guts of omnivores contained mostly detritus (e.g. plant material and bacteria; mean  $\pm$  SEM percent volume =  $60.4 \pm 10.4\%$ ) followed by anostracan fairy shrimp ( $37.5 \pm 10.4\%$ ) and algae ( $2.2 \pm 0.6\%$ ), whereas those of carnivores contained mostly fairy shrimp ( $84.9 \pm 2\%$ ) followed by detritus ( $13.6 \pm 2.1\%$ ) and algae ( $1.6 \pm 0.7\%$ ). Additionally, diet plays a role in inducing carnivores. *Spea* tadpoles are normally born as omnivores, becoming carnivores only when they ingest shrimp (Pfennig 1990). However, different sibships vary in carnivore production, even when reared under common conditions, pointing to heritable variation in morph

expression (Ledón-Rettig & Pfennig, 2011). Moreover, previous research has revealed that competitively-mediated disruptive selection has likely acted on this variation to favour carnivore-omnivore polymorphism (Pfennig, Rice & Martin, 2007; Martin & Pfennig, 2009).

We combined stable isotope analyses of tadpoles from natural populations with a controlled experiment aiming to characterize dietary differences between these alternative carnivore and omnivore morphs and to assess the potential ecological consequences of any such differences. Our data suggest that resource-use specialists may indeed experience greater competition than resource-use generalists.

## MATERIAL AND METHODS

### STABLE ISOTOPE ANALYSIS

Although Pomeroy (1981) compared the gut contents of omnivores and carnivores, gut contents only reveal what individuals ate recently and therefore do not measure potential lifetime dietary differences between individuals. Additionally, and perhaps more importantly, gut contents only reveal what individuals consume and not what they actually assimilate. To characterize dietary differences between morphs, we therefore performed stable isotope analyses.

We began by collecting tadpoles from four ponds near Portal, AZ, approximately 16 days after each pond filled and approximately 14 days posthatching (in all ponds, all eggs were laid on the same day; tadpoles began to metamorphose at around 16 days posthatching). In all ponds, *S. multiplicata* was the only species of *Spea* present. We collected tadpoles from randomly selected sites throughout each pond using a handheld dip net. Immediately after collection, we euthanized the tadpoles by immersion in a 0.1% aqueous solution of tricane methanesulfonate (MS 222). Tadpoles were then frozen on dry ice and shipped to the University of North Carolina, where they were prepared for morphological and stable isotope analyses.

To categorize each field-caught tadpole by morphotype, we followed the methods of Pfennig *et al.* (2007). Briefly, we first measured each tadpole's mass and snout-vent length (SVL). We then measured the width of the orbitohyoideus (OH) muscle and characterized the shape of each tadpole's keratinized mouthparts (MP). In addition, we counted the number of rows of labial teeth (LT; Martin & Pfennig, 2009) and approximated the length of each tadpole's intestines by counting the number of gut coils (GC). We standardized OH for body size (SVL) by regressing  $\ln$  (i.e. natural log) OH on  $\ln$  SVL and used the resulting residuals for the subsequent analyses. We then

combined MP, LT, GC, and the residuals of  $\ln$  OH regressed on  $\ln$  SVL, pooling tadpoles from all four ponds together, into a single multivariate shape variable (the ‘morphological index’; Pfennig *et al.*, 2007) by calculating a principal-component (PC) score on the correlation matrix. From this analysis, we used PC1 as our morphological index, where PC1 explained 70% of the variance in tadpole morphology. Tadpoles with greater values of PC1 tend to possess more carnivore-like morphology, with larger OH muscles, more keratinized MP, fewer LT, and fewer GC, whereas tadpoles with lesser values tend to possess more omnivore-like morphology.

We then determined whether the morphological indices in each pond were distributed bimodally. To do so, we followed the methods presented in Martin & Pfennig (2010) by using the framework and software described in Brewer (2003). Within this Bayesian framework, we tested the hypothesis that the mixture of two normal distributions fit the data better than a single normal distribution. To evaluate this hypothesis, we used Akaike’s information criteria (AIC) corrected for sample size (Burnham & Anderson, 2002). Specifically, we calculated  $\Delta AIC_c$  by taking the difference between  $AIC_c$  of the fitted single normal distribution minus  $AIC_c$  of the mixture of two normal distributions. We interpreted  $\Delta AIC_c > 4$  as indicating more support for the fit of a mixture model than the fit of a single normal distribution, whereas  $\Delta AIC_c$  between  $-4$  and  $4$  indicated equivalent support for the fit of the mixture model and single normal distribution, and  $\Delta AIC_c$  less than  $-4$  as more support for the fit of a single distribution (Burnham & Anderson, 2002). The distribution of morphological indices was significantly bimodal in all four ponds (see Supporting information, Figs S1, S2; Table S1). Therefore, to classify each tadpole as a carnivore or omnivore, we determined the morphological index value that corresponded to the minimum inflection point between the two modes of the overall distribution (see Supporting information, Fig. S2). We then categorized each tadpole as either an omnivore or a carnivore based on which side of this minimum point that particular tadpole fell. If a tadpole’s morphological index fell below this minimum value, it was categorized as an omnivore; if it fell above this minimum value, it was categorized as a carnivore.

Finally, we used stable isotope analysis to infer the diets of each of our field-caught tadpoles (and, thus, of the two morphs). Stable isotopes analysis of muscle tissue records long-term dietary information for individual tadpoles (Dalerum & Angerbjorn, 2005; McIntyre & Flecker, 2006), which reduces the potential for stochastic effects. We examined nitrogen stable isotopes ( $\delta^{15}\text{N}$ ). Measures of  $\delta^{15}\text{N}$  indicate an organism’s trophic positions in a food web (Post, 2002), which

appears to be the primary dietary axis along which carnivores and omnivores differ (see Introduction). To perform these analyses, we used the tadpoles from the collections described above ( $35.75 \pm 3.8$  tadpoles from each of four ponds or 143 tadpoles in total; 60 carnivores and 83 omnivores). We then obtained muscle tissue by removing the entire tail of each tadpole. Tail tissue samples were dried in an oven at  $60^\circ\text{C}$  for 48 h. A sample ( $1.0 \pm 0.2$  mg) of dried tissue was placed into a silver capsule ( $5 \times 9$  mm) and submitted to the University of California at Davis Stable Isotope Facility for analysis (detailed procedures, see the Supporting information, Doc. S1).

From the stable isotope data, we were able to infer the trophic structure of the *Spea* resource polymorphism. Specifically, we used box plots to infer the median, minimum, and maximum  $\delta^{15}\text{N}$  values, as well as the 25th and 75th percentiles for each morph classification. This also allowed us to determine the relative trophic levels that each group occupied and to examine the range of  $\delta^{15}\text{N}$  values within each morph, which we interpreted as each morph’s trophic breadth.

We first scaled each tadpole’s  $\delta^{15}\text{N}$  value to the shrimp  $\delta^{15}\text{N}$  value from its pond. We did so by subtracting each tadpole’s  $\delta^{15}\text{N}$  value from that of the  $\delta^{15}\text{N}$  value for shrimp that were collected from that pond (shrimps were sampled at the same time as the tadpoles from each pond). We performed this correction to control for any environmental variation that might cause  $\delta^{15}\text{N}$  values to differ between ponds (i.e. shrimp might differ from pond to pond, which would cause tadpoles from different ponds also to differ, even though their diets might actually be similar). We combined all the tadpoles from each pond into one analysis and then used the box plots to compare trophic breadth between morphs.

We statistically tested the hypothesis that omnivores and carnivores differed across all ponds in diet with a linear mixed model with the corrected  $\delta^{15}\text{N}$  as our response variable, morphotype classification as our predictor variable, assuming unequal variances between groups, and pond origin as a random intercept fit using restricted maximum likelihood, which produces unbiased estimates of the variance components (Pinheiro & Bates, 2000). We also statistically tested the hypothesis that omnivores and carnivores differed across all ponds in trophic breadth. To do so, we compared the variances of the corrected  $\delta^{15}\text{N}$  for each morph.

Finally, for each morph and in each pond, we evaluated whether a tadpole’s morphology reliably predicted its resource use, as measured by its corrected  $\delta^{15}\text{N}$  value. These data were used to infer the possible existence of individual specialization (as revealed by a significant relationship between each tadpole’s morphological index and its  $\delta^{15}\text{N}$  value).

COMPARING INTRA-MORPH COMPETITION FOR  
EACH MORPH

Because our stable isotope analyses suggested that carnivores utilize a narrower range of resources than do omnivores (see Results), we used a controlled experiment to determine whether intramorph competition is greater among these resource-use specialists than among the more generalist omnivores. To do so, we analyzed data from a previously published experiment (Martin & Pfennig, 2009). This experiment was originally designed to test whether intraspecific competition is more intense the more similar any two conspecific competitors are to each other in resource use. In the present study, we re-analyzed the data to determine whether intramorph competition is less intense for more omnivore-like individuals than for carnivore-like individuals.

In this earlier experiment, pairs of tadpoles were reared together in laboratory microcosms and given limited amounts of the two main resources: detritus and shrimp. We measured the growth of tadpoles and determined whether tadpoles grew less the more similar they were to their tankmate in resource use. This experimental set-up mimics conditions tadpoles likely frequently experience in the wild. In many natural ponds, both carnivores and omnivores are present (often in almost equal proportions), these ponds typically contain only two main resource types (detritus and shrimp), and these resources are almost always limited, ensuring intraspecific competition for these food items (Martin & Pfennig, 2009, 2010).

Randomly selected 2-week old *S. multiplicata* tadpoles were weighed and assigned to one of two treatment groups: (1) an experimental group, in which two unrelated tadpoles were placed together in a tank, and (2) a control group, in which one tadpole was placed alone in a tank. Similar-sized siblings were placed in adjacent experimental and control tanks, thereby allowing for a comparison of growth of siblings whose rearing environments were similar in all respects, except for the presence or absence of a potential competitor. Once the experiment began, each experimental tank received 20 live brine shrimp once a day and 20 mg of crushed fish food every other day (fish food simulates in form and nutrition the detritus on which these tadpoles feed in natural ponds; Pfennig, Rice & Martin, 2006). Control tanks received half the amount of food as experimental tanks, such that the per capita amount of food provided to both treatments was identical. In all experimental tanks, shrimp and detritus had disappeared by the time the tadpoles were fed again, ensuring that competition had taken place. The experiment ended after 7 days, at which point we again measured the mass of each tadpole. Before starting the experiment, we measured the time it took

for each tadpole in the experimental tanks to eat three fairy shrimp. Shrimp-eating time is a highly repeatable measure, and tadpoles that are most similar in time to eat shrimp are most likely to compete for food (Pfennig *et al.*, 2007). Moreover, this measure predicts a tadpole's propensity to ultimately develop the carnivore morphology (Pfennig *et al.*, 2007).

We analyzed a subset of data from this experiment that included the experimental tankmates that were most similar in predilection to consume shrimp (i.e. tankmates that differed by less than 60 min in shrimp-eating time). Because tankmates that differed by more than 60 min in shrimp-eating time were also likely to differ substantially in resource use (i.e. be composed of pairings between more omnivore-like and more carnivore-like tadpoles), they were not informative for addressing our question, and we therefore excluded them from this analysis.

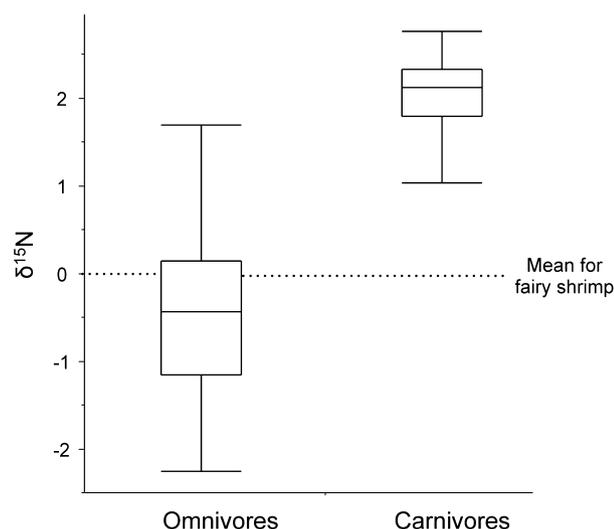
Using the tadpoles in this subset of 31 experimental tanks, we measured how the intensity of competition varies between the more carnivore-like experimental pairs (those that consumed all three shrimp in a shorter period of time) and the more omnivore-like experimental pairs (those that consumed all three shrimp in a longer period of time). Our response measure was each experimental tadpole's percentage growth during the course of the experiment (final mass/initial mass), controlling for that of its matched control sibling. In particular, we subtracted, from each experimental tadpole's percentage change in mass, the percentage change in mass of its matched sibling in a neighbouring control tank. Thus, values < 0 indicated that the focal tadpole reared in competition grew less than did its sibling reared alone. By contrast, values > 0 indicated that the focal tadpole reared in competition grew more than did its sibling reared alone.

If competition is less intense for more omnivore-like pairs of tadpoles than for more carnivore-like pairs of tadpoles, then growth (adjusted percentage change in mass) of experimental tadpoles should be higher the more omnivore-like (longer shrimp-eating times) experimental tankmates were. To test this prediction, we fit a linear model with the adjusted percentage change in mass for all experimental tadpoles within the 60-min subset as the response, our measure of morphotype (mean time to eat three shrimp for each experimental pair) as a predictor, and the absolute value of the difference in mean shrimp-eating time for each experimental pair as a covariate to account for the variation in shrimp-eating time within each tank.

## RESULTS

### STABLE ISOTOPE ANALYSIS

We found two discrete dietary groups in every pond (see Supporting information, Fig. S3). Overall, carni-



**Figure 1.** Box plots of stable isotope ( $\delta^{15}\text{N}$ ) values for omnivores ( $N = 83$  individuals) versus carnivores ( $N = 60$  individuals) from four different ponds. Box plots show median (horizontal lines), 25th and 75th percentiles (top and bottom of box), and range (whiskers, excluding outliers).

vores and omnivores differed significantly in mean  $\delta^{15}\text{N}$  values, with carnivores consuming resources from a higher trophic level than omnivores (Fig. 1). Indeed, the overall (i.e. across all ponds) mean  $\pm$  SEM  $\delta^{15}\text{N}$  value for carnivores ( $2.05 \pm 0.09$ ) was significantly greater than that for omnivores ( $-0.47 \pm 0.07$ ;  $F_{1,138} = 106.45$ ,  $P < 0.0001$ ). Moreover, omnivores and carnivores differed significantly in trophic breadth: carnivores possessed a narrower range of  $\delta^{15}\text{N}$  values (SD for carnivores: 0.44) than did omnivores (SD for omnivores: 0.84;  $F_{82,59} = 3.56$ ,  $P < 0.0001$ ). Overall, the range of  $\delta^{15}\text{N}$  values for carnivores (1.81 units) was less than half that of omnivores (3.95 units; Fig. 1).

Additionally, we found evidence of a fine-scale relationship between resource use and morphology for omnivores but not for carnivores. In particular, in two of the four ponds, an omnivore's morphological index significantly predicted its  $\delta^{15}\text{N}$  value (Fig. 2). By contrast, in none of the ponds did a carnivore's morphological index predict its  $\delta^{15}\text{N}$  value (data for all ponds combined;  $F_{1,58} = 0.70$ ;  $P = 0.40$ ; data for individual ponds are presented in the Supporting information, Fig. S4).

#### COMPARING INTRA-MORPH COMPETITION FOR EACH MORPH

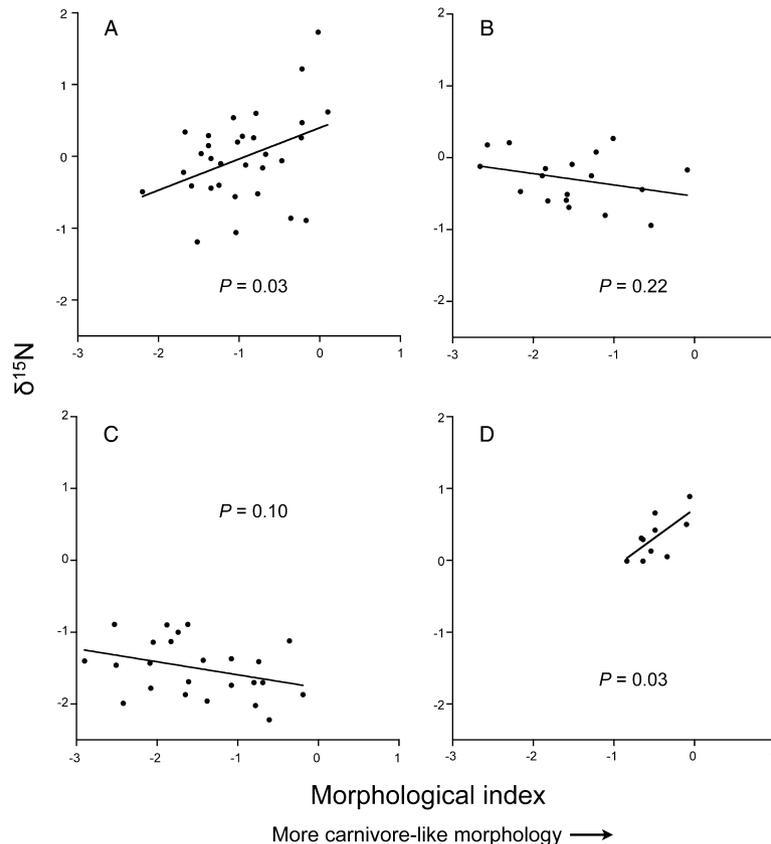
We found a significant linear relationship between our proxy of morphotype for each experimental pair (i.e. each tadpole's mean time to eat shrimp) and the focal tadpole's growth ( $F_{1,28} = 6.16$ ;  $P = 0.019$ ). Specifi-

cally, when competitors were the most omnivore-like in their foraging behaviour, the focal tadpole grew the most. By contrast, when competitors were the most carnivore-like in their foraging behaviour, the focal tadpole grew the least (Fig. 3). These results could not be ascribed to any intrinsic differences in growth rates between omnivores and carnivores: we measured growth as the percentage change in mass of the focal animal, accounting for the percentage change in mass of its matched sibling that was not experiencing competition (meaning that we were not directly comparing absolute growth between omnivores and carnivores). Thus, competition was more intense among carnivores (the trophic specialists) than among omnivores (the trophic generalists).

#### DISCUSSION

In spadefoot toad tadpoles, morphological traits serve as predictors of diet, as has been reported in fish and insects (Bolnick & Paull, 2009; Barton *et al.*, 2011). Indeed, by analyzing nitrogen stable isotopes of wild-caught tadpoles, we found that alternative carnivore and omnivore morphs differ in trophic breadth, with carnivores exhibiting narrower trophic breadth, as well as occupying a higher trophic level, than omnivores (Fig. 1). Moreover, a controlled experiment revealed that more carnivore-like individuals (as identified by a behavioural assay) experienced greater competition with each other than did more omnivore-like individuals (Fig. 3). We hypothesize that the costs of this increased competition among resource-use specialists may even outweigh the benefits of specialization, thereby possibly precluding the evolution of resource polymorphism in certain populations.

More intense intramorph competition among resource-use specialists likely reflects, in part, functional trade-offs that prevent specialists from successfully utilizing alternative resources when their original resource is depleted. For example, omnivores possess a much longer intestine than carnivores (Pomeroy, 1981; Ledón-Rettig, Pfennig & Nascone-Yoder, 2008). An omnivore's long intestine enables it to process and assimilate plant and bacterial material more effectively than a short-gutted carnivore could. Additionally, omnivores possess numerous labial teeth for rasping biofilm and algae from hard surfaces (Martin & Pfennig, 2009, 2011). These features presumably explain why the more morphologically omnivore-like a tadpole is, the better that individual grows when fed exclusively detritus (Martin & Pfennig, 2009). By contrast, carnivores have morphological features (e.g. keratinized mouthparts and large jaw musculature) that render them more capable of subduing the large, active shrimp prey (Frankino & Pfennig, 2001; Martin & Pfennig, 2009, 2011).

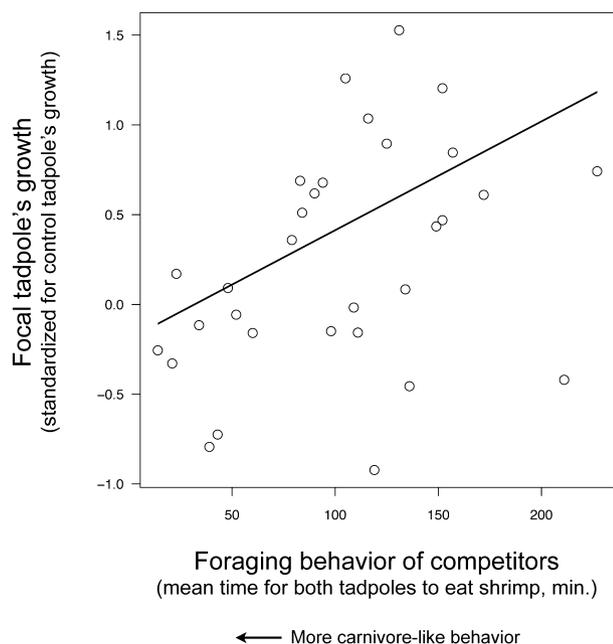


**Figure 2.** Relationship between an omnivore's morphological index and its  $\delta^{15}\text{N}$  values in four ponds: (A) Ava Ranch; (B) Crissal; (C) Peach Orchard North; and (D) Price Canyon. Each dot represents an individual omnivore; least-squares regression lines are shown for illustrative purposes only. Note that a significant relationship exists between trophic morphology and resource use in Ava Ranch and Price Canyon ponds, possibly suggesting individual specialization in these ponds.

Although their distinctive features enable carnivores to take advantage of the ecological opportunity presented by the highly nutritious shrimp resource, these same features may resign carnivores to a life of trophic specialization. In particular, although these features may give carnivores a growth and survival advantage over omnivores early in ontogeny, these same features may be disadvantageous later in ontogeny when the carnivore's shrimp resource becomes scarce. Indeed, shrimp decline in abundance rapidly in natural ponds and are nearly always a limiting resource (Pfennig, 1992). In such circumstances, carnivores may be unable to switch to alternative resources (e.g. detritus or algae) because they are poorly equipped to process resources other than shrimp (Martin & Pfennig, 2009). By contrast, omnivores can consume and assimilate a wide range of food items, including small crustaceans and even the occasional moderate-sized shrimp, as long as they do not have to compete for the latter food items (Frankino & Pfennig, 2001). Therefore, functional trade-offs, coupled with the carnivore's

dependence on an ephemeral, relatively scarce resource, presumably explain why carnivores experience more intense intramorph competition than omnivores (Fig. 3).

In addition to functional trade-offs and resource ephemerality, another factor that likely determines the intensity of intramorph competition (and, hence, whether or not a resource polymorphism evolves) is ecological opportunity, by which we mean the presence of alternative resource types that are underutilized by other species (Martin & Pfennig, 2010). In the presence of ecological opportunity, a population can expand the range of resources that it uses as an adaptive response to intraspecific competition; in some cases, it may even evolve a novel resource-use specialist (Bolnick, 2001). By contrast, in its absence, a novel resource-use specialist is less likely to succeed evolutionarily, and, consequently, resource polymorphism is unlikely to evolve. Indeed, resource polymorphism occurs most often in populations experiencing abundant ecological opportunity (Robinson & Wilson, 1994; Parent & Crespi, 2009; Martin &



**Figure 3.** Experimental evidence that more carnivore-like tadpoles suffer more from competition with each other than more omnivore-like tadpoles do with each other. The relationship is shown between the foraging behaviour of two competitors (as measured by the mean time of both tadpoles to eat shrimp, where more carnivore-like tadpoles eat shrimp faster) and the focal tadpole's growth (as measured by the growth of the focal tadpole compared to its sibling that was treated similarly but did not experience competition).

Pfennig, 2010). Thus, the evolution of resource polymorphism depends on several factors, including functional trade-offs, resource ephemerality, ecological opportunity, and the intensity of intraspecific competition (Pfennig & Pfennig, 2012).

Our results also help explain how a generalist ecomorph can coexist with a specialist ecomorph, even when the latter utilizes the higher-quality (i.e. more profitable) resource type (as is often the case; Smith & Skúlason, 1996). For example, in spadefoot tadpoles, specialists (carnivores) outcompete generalists (omnivores) for shrimp (Frankino & Pfennig, 2001), which is the resource on which these tadpoles grow best (Pfennig, 2000; Pfennig & Murphy, 2000). However, although dietary specialists may benefit (initially) by being able to monopolize the more profitable resource, specialists should experience more intense intramorph competition (Fig. 3), especially as their resource is depleted. In such cases, negative frequency-dependent selection (arising from intraspecific competition) should maintain both specialists and generalists within the same population, such that each morph has, on average, equal fitness (Pfennig, 1992).

Interestingly, in two of the four study ponds, we found a significant positive relationship between morphological index and  $\delta^{15}\text{N}$  among omnivores (Fig. 2) but not among carnivores (see Supporting information, Fig. S4). Indeed, in these two ponds (Fig. 2A, D), omnivores that differed the most from carnivores morphologically also differed the most from carnivores in diet; omnivores that were intermediate in morphology were also intermediate in diet; and omnivores that were the most similar to carnivores morphologically were also the most similar in diet. In other words, although omnivores as a group are dietary generalists, individuals may specialize on different food items (or on different combinations of the same array of food items). Such individual specialization reduces pairwise dietary overlap between individuals, which can lessen the intensity of competition (Bolnick *et al.*, 2003; see also below). In the two ponds where individual specialization was detected, qualitative estimates of resource levels and tadpole densities (Martin & Pfennig, 2010) indicated that per capita resource abundance was lowest (see Supporting information, Table S2), suggesting that intraspecific competition may have indeed been most intense in these ponds.

Our data therefore clarify how competitively-mediated selection drives divergence in both diet and morphology among specialists versus among generalist. Omnivores displayed high variation in diet (Fig. 1) and (in two of the four ponds) a fine-scale relationship between diet and morphology (Fig. 2A, D). Thus, selection for more extreme omnivores may reflect selection for dietary divergence, which allows individuals to avoid competition with other omnivores by consuming slightly different resources. In carnivores, by contrast, we found no (obvious) fine-scale relationship between diet and morphology (see Supporting information, Fig. S4). Therefore, rather than favouring carnivores that are increasingly more divergent from other carnivores in diet, competitively-mediated selection may favour competitively superior carnivores. Indeed, carnivores with larger morphological index values subdue shrimp more easily and therefore outcompete carnivores with lower morphological index values (Martin & Pfennig, 2009). Competitively-mediated selection may therefore reduce intramorph competition differently among specialists than among generalists.

In sum, in a population containing alternative resource-use morphs, where one is a generalist and the other is a novel specialist morph, the latter may often experience more severe intramorph competition. Generally, whether or not a resource polymorphism evolves in any given population may depend, in part, on whether or not the benefits of specialization outweigh the costs of such increased competition among specialists.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Doc. S1.** Procedures and Instruments used by the UC Davis Stable Isotope Facility.

**Figure S1.** Density histograms and fitted kernel density lines of trophic morphology for tadpoles in each of four ponds: (a) Ava Ranch, (b) Crissal, (c) Price Canyon, and (d) Peach Orchard North.

**Figure S2.** Density histograms and fitted kernel density lines of trophic morphology for tadpoles in all four study ponds combined.

**Figure S3.** Resource use, as inferred by  $\delta^{15}\text{N}$ , plotted against morphological index for individual carnivores and omnivores in four ponds.

**Figure S4.** Relationship between a carnivore's morphological index and its  $\delta^{15}\text{N}$  values in four ponds.

**Table S1.** Estimates of bimodality of tadpole morphological indices in natural ponds.

**Table S2.** Estimates of tadpole densities and morph frequencies in natural ponds.