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TRADE-OFF BETWEEN COMPETITIVE ABILITY AND ANTIPREDATOR ADAPTATION IN A FRESHWATER AMPHIPOD SPECIES COMPLEX

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Abstract. Body size influences many physiological and ecological processes, and thus adaptive change in body size may hold diverse consequences for individuals. For amphipods in the *Hyalella azteca* species complex, divergence in body size appears to be driven by adaptation to disparate regimes of size-biased mortality experienced in different habitat types. Here I ask how size and size-related traits influence competitive ability of large-bodied and small-bodied species. I examined competitive ability in both species using a factorial experiment in which the performance of each species was assessed in all combinations of the presence and absence of the heterospecific amphipod species crossed with the presence and absence of a snail species. Results demonstrated that the large and small *Hyalella* species differ substantially in competitive ability, with the large species being the superior general competitor. The competitive effect of the large species on the small species was substantial and caused significant reductions in abundance, body size, and fecundity of the small species. In contrast, performance of the large species was not affected significantly by presence of the small species. This competitive asymmetry was also seen in competitive interactions with snails. The small species appears to “trade off” competitive ability in order to survive in habitats with predatory fish, whereas the large species, which is able to obtain a size refuge from predation, has traits that confer strong competitive ability. Because of habitat differences in the cost–benefit structure of the trade-off, however, competition-mediated natural selection may be more intense in the large species than in the small species, a condition that may enhance evolutionary divergence in body size.

Key words: activity level; adaptation; amphipod; body size; competition; fecundity; foraging rate; *Hyalella azteca*; *Physella virgata*; predation; snail; trade-off; competitive ability vs. antipredator adaptation.

INTRODUCTION

Body size affects many physiological and ecological process (Calder 1984, Werner and Gilliam 1984, Sibly and Calow 1986), and thus adaptive change in size invariably involves balancing fitness trade-offs that result from conflicting selection pressures (Roff 1986, 1992). Ecological interactions, such as size-dependent predation (Travis et al. 1985, Tessier et al. 1992, Wellborn 1994a) and competition (Vanni 1986, Werner 1994, Petren and Case 1996, Sabo and Pauley 1997, Kreutzer and Lampert 1999), may be especially important in shaping adaptive changes in body size (Edley and Law 1988, Spitze 1991, Schluter and McPhail 1992) because of the ubiquity of these interactions in nature. Body size adaptation will thus involve balancing size-specific costs and benefits that will, in general, differ across diverse ecological settings. Understanding these trade-offs between antipredator adaptation and competitive ability provides insight into ecological and evolutionary dynamics in heterogeneous landscapes (McPeck 1996, Wellborn et al. 1996, Wissinger et al. 1999). Species distributions, for example, are often

shaped by a few fundamental fitness trade-offs (Tilman 1988, Wellborn et al. 1996). Traits that allow a species to be successful in some habitats can prevent the species from occurring in ecologically dissimilar habitats, leading to the development of alternative community types across environmental gradients (Wellborn et al. 1996, Leibold et al. 1997). Also, depending on their specific properties, fitness trade-offs may act to promote species diversification for taxa distributed across heterogeneous environments (Schluter and McPhail 1992), or, alternatively, may impede diversification by restricting the selective environment experienced by populations (McPeck 1996).

This study examines the consequences, with respect to competitive ability, of an adaptive divergence in body size in two species within the *Hyalella azteca* species complex (Amphipoda: Hyalellidae). These amphipods are common grazers in freshwater habitats of North America (Bousfield 1973), and recent studies have documented diversification within the group (Wellborn 1994a, 1995, Thomas et al. 1997, Hogg et al. 1998, McPeck and Wellborn 1998, Witt and Hebert 2000). Within this species complex there is a striking pattern of habitat-specific morphological and life history differentiation consistent with adaptive diversification (Wellborn 1994a, 1995). In fishless habitats, mortality is greatest for small individuals and decreases

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with body size. *Hyalella* here mature at a large size, and reach a size refuge from predation. In habitats with centrarchid fish, mortality increases with body size due to size-selective predation by fish. *Hyalella* in these habitats mature at a small size and maintain a small adult body size. The observed body size and life history differences are consistent with those expected for adaptation under these disparate mortality schedules (Law 1979, Edley and Law 1988, Taylor and Gabriel 1992). Because these species have not been formally described, I will refer to them here as "large" and "small" *Hyalella* species.

METHODS

I examined competitive ability of large and small *Hyalella* species in a 2×2 factorial experiment that included all four combinations of the presence and absence of the heterospecific amphipod species crossed with the presence and absence of a pulmonate snail, *Physella virgata* (Gastropoda: Physidae). Treatments involving direct interaction of the two amphipod species assess the form and magnitude of competitive interactions between the species, and treatments involving interactions between each amphipod species and the snail provide an independent and standardized assessment of competitive ability with the same competitor. *Physella virgata* is abundant, coexists with both *Hyalella* species, and is likely to compete with *Hyalella* because physid snails are able to depress grazer resources (Doremus and Harman 1977, Brown et al. 1994, McCollum et al. 1998). Amphipods used in the experiment are representative (based on morphology, life history, and allozyme affiliation) of the common small and large species in Oklahoma (*unpublished data*). Individuals of the small *Hyalella* species were collected in McClain County, Oklahoma from a pond that contains predatory fish, including bluegill (*Lepomis macrochirus*). The large *Hyalella* species and the snails were collected from a small, fishless stream in Marshall County, Oklahoma.

The experiment was conducted in a greenhouse, and experimental units were 20.8-L aquariums filled with 18 L of tap water. Beach sand (150 mL) was added to form a bottom substrate. Additionally, 2 L of lake water was added to provide an initial community of algae, and a moderately low concentration of nutrients (52.2 mg KPO_4 , 338.3 mg NH_4NO_3) was added to encourage growth of algal resources for the amphipods and snails. Aquariums were randomly assigned to treatments, and there were five replicates for each experimental treatment. Amphipods were stocked at an initial density of 60 adults of the appropriate species. The design was additive, thus mixed-species treatments received 60 individuals of each amphipod species. Fifteen adult snails were added to each aquarium assigned to a snails-present treatment. The stocking density for amphipods in this experiment (equivalent to 750 amphipods/m²) was less than typical natural densities (~2000–12 000 am-

phipods/m² [Wellborn 1994a]). My intention was to initiate this experiment with a relatively low density of amphipods and allow the populations to grow under the influence of the interspecific interactions. The experiment was terminated after 40 d, enough time for stocked females to produce multiple clutches and for second generation females to begin reproducing. Snails also reproduced during the experiment, but offspring did not reach maturity.

Adults of the two *Hyalella* species used in this study can be distinguished by the presence of a dorsal mucronation on pleon segment two of the large species that is lacking in the small species (*unpublished data*). Below ~0.38-mm head length, however, the species are indistinguishable, and I therefore restrict my analysis to adults. Because a large number of adult amphipods were recovered from the tanks, I adopted a random subsampling procedure to select amphipods for measurement. I first established eight random subsamples by pouring the entire sample of amphipods and snails from an aquarium into a 85 mm diameter petri dish divided into eight equal sections. I then established a sub-subsample by pouring the contents of one randomly selected subsample into a sectioned petri dish, and randomly selected one of the sections to obtain amphipods to be measured. I repeated this process for two additional subsamples, and the three sub-subsamples from an aquarium were combined for analysis. Due to a low abundance of the small amphipod species in the treatment that included the presence of both the large species and snails, I supplemented the original sub-subsamples by measuring all individuals in an additional randomly selected full subsample. For amphipods, I measured abundance, head length (a measure of body size [Edwards and Cowell 1992]), and fecundity (number of eggs in a female's brood chamber). Snails were enumerated by counting all individuals in the three original subsamples used for selecting amphipods.

For each amphipod species, I used a two-factor MANOVA to test for effects of the presence vs. absence of both the heterospecific species and snails, and for the interaction of these factors. The analysis was performed with the GLM procedure in the SYSTAT 7.0 statistical package (Wilkinson 1997) and both factors were considered fixed effects. Response variables in the analysis were abundance (log-transformed), mean head length, and mean fecundity. Together, these response variables provide an index of the overall performance of amphipods under the experimental treatments. I used MANOVA both to control Type I error and assess effects on overall performance through a set of response variables that are likely to be correlated (Wellborn 1994a). To evaluate which response variables contributed most heavily to significant treatment effects in the MANOVA, I examined standardized canonical coefficients and performed univariate tests for each response variable. Standardized canonical coef-

ficients quantify the weighting of each response variable in the dominant eigenvector in MANOVA, and thus describe the relative contribution of response variables to the effects observed for each factor (Scheiner 1993). The univariate tests assess each response variable independent of its correlation with other response variables. To determine whether the amphipod species differed in their competitive effect on snails, I used one-way ANOVA to compare snail abundance (log-transformed) in the presence of the large vs. small amphipod species.

RESULTS

In the absence of interspecific interactions, abundance of both amphipod species increased to ~900 adults per aquarium (equivalent to 11 250 adults/m²), indicating that relatively high rates of population increase were possible under the experimental conditions (Figs. 1 and 2). The performance of the small species was depressed by the presence of both the large species and snails (Table 1). The effect of the large species was substantial, causing a sevenfold reduction in the final abundance of the small species (Fig. 1a), a 0.040-mm reduction in mean head length (Fig. 1b), and a 25-fold reduction in fecundity (Fig. 1c). Snails had a significant competitive effect on the small species (Table 1), but this effect was much weaker than that of the large amphipod species (Fig. 1). Both standardized canonical coefficients and the univariate analyses (Table 1) indicate that the primary effect of snails was to cause a moderate reduction in abundance of the small species (Fig. 1a). In the combined-competitor treatment, mean abundance of the small species declined to 30.3 ± 6.98 individuals (mean ± 1 SE), approximately one-half of the initial stocking density, and none of the sampled females carried eggs.

The large species was not affected by the presence of the small species, but did exhibit a significant multivariate response to the presence of snails (Table 1, Fig. 2). Standardized canonical coefficients (Table 1) indicate that the effect of snails on the large species was complex, resulting from the combination of reduced abundance (Fig. 2a) but increased fecundity (Fig. 2c) in the presence of snails, although neither response variable was significant when tested individually (univariate tests, Table 1).

Few of the originally stocked adult snails remained at the end of the experiment, but their juvenile progeny were very abundant. Thus treatment differences in final snail density primarily reflect differences in adult reproduction and juvenile survival. Snail density was significantly lower in the treatment with the large *Hyalella* species than in the treatment with the small *Hyalella* species ($F = 10.65$, $df = 1, 8$, $P = 0.011$, Fig. 3).

DISCUSSION

Large and small *Hyalella* species differ substantially in competitive ability, with the large species being the

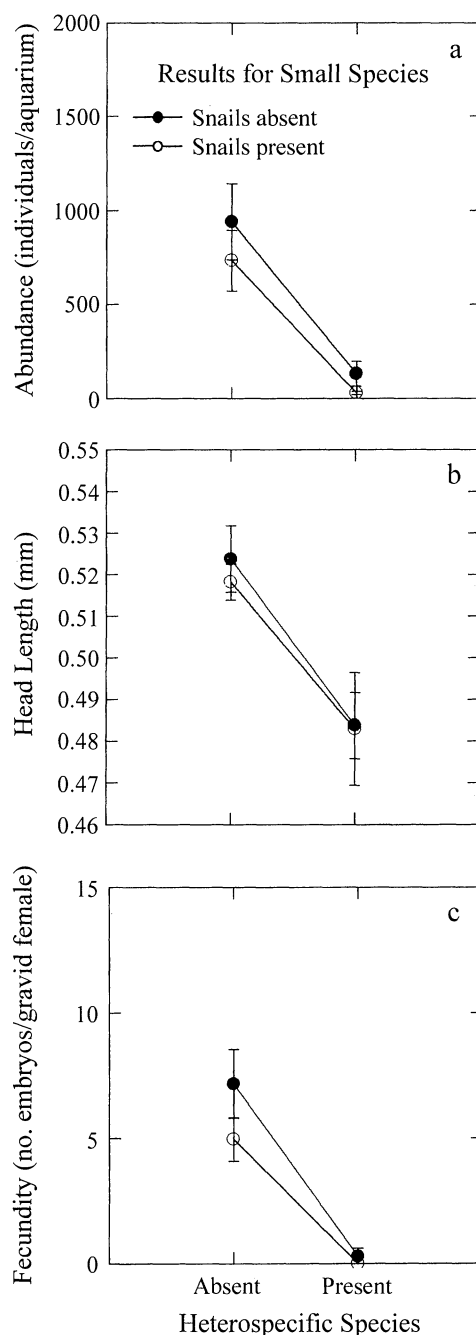


FIG. 1. Abundance, head length, and fecundity of the small *Hyalella* species in the presence vs. absence of the heterospecific (large) species and presence vs. absence of snails. Data are means ± 1 SE.

superior general competitor. Competitive effects of the large species on the small species were very strong for each measure of performance. If one compares the small species' performance in the absence of interspecific competition to its performance in the presence of the large species, competition caused reductions of 3.1 pooled standard deviations (SD) in abundance, 2.5 SD

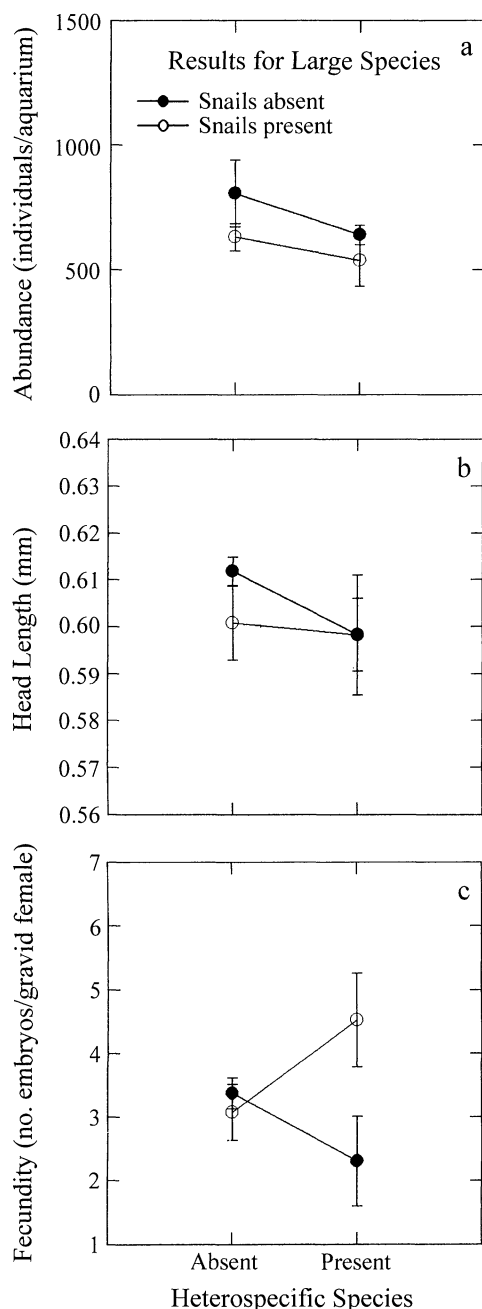


FIG. 2. Abundance, head length, and fecundity of the large *Hyalella* species in the presence vs. absence of the heterospecific (small) species and presence vs. absence of snails. Data are means \pm 1 SE.

in body size, and 4.1 SD in fecundity. In contrast to the large reduction in performance suffered by the small species in the presence of the large species, performance of the large species was not significantly affected by presence of the small species. Thus, when assessed through treatments in which they interact directly, competitive abilities of the two species are strongly asymmetrical.

Asymmetry in competitive ability between *Hyalella* species was also evident in their interactions with snails. Relative to the small species' impact on snails, the large species caused a 46% reduction in snail abundance. Because the outcome of the interactions between amphipod species and a common competitor, the snail *P. virgata*, can serve as an indicator of the general competitive ability of the amphipods, this result suggests that the stronger competitive effect of the large species is a general attribute of the large species, and is not an idiosyncratic effect in the interaction between the two amphipods. Snails significantly affected performance of both *Hyalella* species, but the effects were moderate in magnitude. The abundance of both amphipod species was reduced by an identical 22% in the presence of snails. Additionally, based on the standardized canonical coefficients from MANOVA, reduced fecundity of the small species contributed moderately to the significant multivariate effect of snails on the small species, but, for the large species, increased fecundity contributed substantially to the multivariate effect of snails (perhaps as a compensatory response to lower intraspecific density in the combined-competitor treatment). To some degree, the comparatively moderate effect of snails may have resulted from the snails' broader use of space in the aquariums. Whereas amphipods used the bottom substrate almost exclusively, snails were commonly seen on aquarium walls and the water surface, as well as on the bottom substrate.

Body size, competitive ability, and trade-offs

The body size disparity between the small and large species probably accounts for the pronounced asymmetry between species in competitive ability. Although size disparity between potential competitors can abate competitive effects when it is associated with reduced overlap in diet composition or other resource axes (Schluter and McPhail 1992), size disparity can lead to asymmetrical exploitative and interference competition when overlap in resource use is high (Neill 1984, Rabeni 1985, Petren and Case 1996, Robertson 1996, Kreutzer and Lampert 1999). Amphipods in the *Hyalella azteca* species complex are generalist grazers on periphyton and detritus (Hargrave 1970, DeMarch 1981), and thus the large and small species examined in this study probably have high overlap in diet composition that is independent of body size.

In *Hyalella*, two size-related behaviors may underlie much of the asymmetry in competitive ability observed between large and small species. First, resource consumption rate increases with body size in both species, but when size-specific resource consumption rates are weighted by the size frequency of individuals in natural populations, a typical individual of the large species has an approximately fourfold greater impact on resources than an individual of the small species (Wellborn 1994b). Thus the size allometry of resource con-

TABLE 1. Summary of two-factor MANOVA examining effects of competition in large and small species within the *Hyalella azteca* species complex.

A) Multivariate tests					
Source of variation	df	Wilks' lambda	<i>F</i>	<i>P</i>	
Small species					
Presence of large species	3, 14	0.072	60.05	<0.001	
Presence of snails	3, 14	0.550	3.81	0.034	
Large species × snails	3, 14	0.786	1.27	0.32	
Large species					
Multivariate test					
Presence of small species	3, 14	0.666	2.34	0.12	
Presence of snails	3, 14	0.489	4.88	0.016	
Small species × snails	3, 14	0.678	2.22	0.13	
B) Standardized canonical coefficients from MANOVA, and univariate tests					
Effect	Variable	Standardized canonical coefficient	df	<i>F</i>	<i>P</i>
Small species					
Presence of large species	abundance	0.833	1, 16	104.15	<0.001*
	body size	0.027	1, 16	22.40	<0.001*
	fecundity	0.706	1, 16	65.76	<0.001*
Presence of snails	abundance	0.913	1, 16	7.59	0.014*
	body size	−0.199	1, 16	0.162	0.69
	fecundity	0.687	1, 16	2.95	0.10
Large species					
Presence of snails	abundance	0.975	1, 16	0.048	0.094
	body size	0.666	1, 16	0.54	0.47
	fecundity	−0.964	1, 16	3.74	0.071

Notes: Factors are presence vs. absence of the heterospecific amphipod and presence vs. absence of snails. Response variables are abundance, mean body size, and mean fecundity. Results of univariate tests and standardized canonical coefficients from MANOVA are provided for those effects determined to be significant in multivariate tests.
* For univariate tests only, an asterisk indicates those effects that are significant under the sequential Bonferroni criteria (at experiment-wise error rate within species of 0.05).

sumption rate creates an inherent asymmetry between species in their per capita impact on resources, and such asymmetry can be an important component of species differences in competitive ability (Petren and Case 1996, Kreutzer and Lampert 1999). Second, activity level increases with body size in both species, but because of the size disparity between species, adults

of the large species are about twice as active as adults of the small species (Wellborn 1993). This greater activity level of the large species probably contributes to its competitive advantage by allowing more efficient or more aggressive foraging. Numerous studies have found a positive association between activity level and competitive ability (Woodward 1982, 1983, Werner 1991, Skelly 1995, Wissinger et al. 1999), and several have explored specific mechanisms underlying this association. For example, more active individuals may be able to more rapidly usurp available resources (Petren and Case 1996) or may be able to more effectively avoid local resource depletion (Werner and Anholt 1993). As these examples make clear, foraging rate and activity level do not contribute independently to species differences in competitive ability. Rather, higher activity level is probably the mechanism by which foraging rate is enhanced. Additionally, resource consumption rate may be influenced by other size-dependent traits, such as differences in size of trophic structures and gut capacity. Together, these size-mediated species differences suggest that body size is of primary importance in the competitive asymmetry between large and small species.
To the extent that disparity in competitive ability between these species results from the difference in

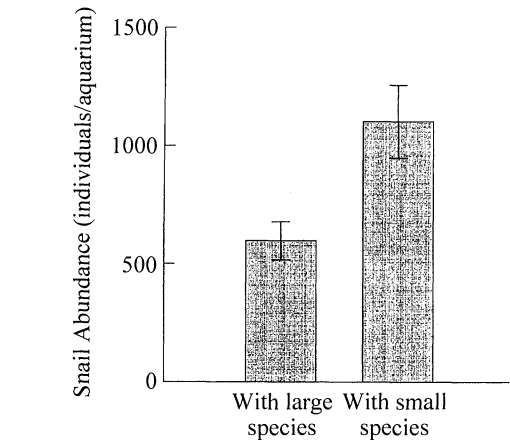


FIG. 3. Abundance of snails (*Physella virgata*) in the presence of the large vs. small *Hyalella* species. Data are means ± 1 SE.

body size, the small species may be thought of as “trading off” competitive ability in order to enhance its ability to coexist with fish. Small body size, coupled with early maturation and high reproductive investment, is crucial to the small species’ success in habitats with centrarchid fish (Wellborn 1994a). In these habitats, predation intensity is considerable and can limit the density of *Hyaella* (Mittelbach 1988, Wellborn and Robinson 1991). Fish predation is also highly size selective, with adults about five times more likely to be consumed than juveniles (Wellborn 1994a). The small species of *Hyaella* persists in the face of fish predation, however, by initiating reproduction at a small body size, maintaining a high size-specific investment in reproduction, and growing slowly after maturity (Wellborn 1994a, b). Additionally, low activity levels may enhance survival with fish, as is the case for many species in these habitats (Wellborn et al. 1996). Thus, the advantages of evolution of a larger body size to enhance competitive ability may be outweighed by the cost of greater predation mortality. In contrast to the small species, the large species does not appear to face a substantial trade-off between competitive ability and predator avoidance in the fishless habitats that they occupy. In fishless habitats, invertebrates, especially dragonflies, are the dominant predators, and these tend to consume smaller individuals of the large species (Wellborn 1994a). Adults of the large species mature at a relatively large size, and, as adults, are largely invulnerable to predation from invertebrates. Thus, relatively large size is an advantage for both avoiding predation and enhancing competitive ability, suggesting that trade-offs between these fitness components are comparatively minor in the large species.

Evolution of competitive ability and antipredator traits

Hyaella amphipods in North America have diversified across freshwater habitats ranging from small fishless habitats to lakes and streams containing predatory fish (Wellborn 1995, Wellborn et al. 1996). A prominent feature of the transition from small fishless habitats to large fish-containing lakes is the development of alternative community types that result from strong predator–prey interactions in the regional aquatic food web (Fig. 4). The importance of competitive interactions in shaping the evolution of body size and other traits in the large and small species during diversification between fish and fishless habitats depends on the form and intensity of competition-mediated selection relative to selection imposed by predators and other agents (e.g., Arnold and Wade 1984, McPeck 1996). However, because strong interactions in the regional food web act to limit community composition in these aquatic habitats (Wellborn 1994a, 1995, Wellborn et al. 1996), the set of selective agents acting on any population is constrained to include only a subset of all possible biotic interactions. That is, some species

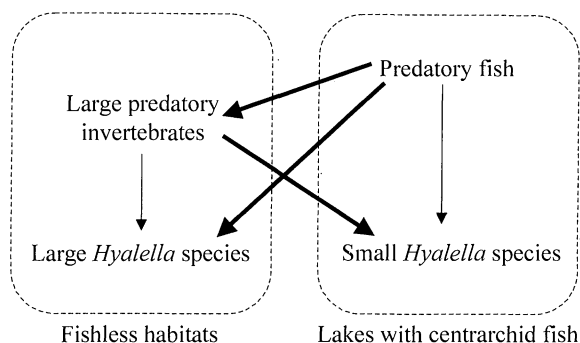


FIG. 4. A simplified regional aquatic food web for the large and small *Hyaella* species. Arrows depict negative predatory interactions, with bold arrows indicating very strong interactions that prevent coexistence and thin arrows indicating moderate interactions that allow coexistence of predator and prey. Considered across the gradient from small fishless habitats to large fish-containing lakes, strong predator–prey interactions in the regional aquatic food web cause the development of alternative community types (demarcated with dashed boxes in the figure). Briefly, alternative community types arise because abiotic constraints limit fish to larger habitats, and distributions of remaining members of the regional species pool are mediated by fundamental fitness trade-offs that affect their ability to deal with fish predation (reviewed in Wellborn et al. [1996]). Habitats that contain centrarchid fish (especially bluegill, *Lepomis macrochirus*) do not contain large, active invertebrates because these species are highly susceptible to fish predation; rather, these habitats contain smaller, less active prey species since these traits foster coexistence with predatory fish. In fishless habitats, large predatory invertebrates such as dragonflies are the top predators, and these predators selectively consume, and thus exclude, the small inactive invertebrates characteristic of fish habitats. Thus characteristics that make species successful in one habitat type are the same traits that exclude them from the alternative habitat type, causing the development of alternative communities across the gradient.

within the regional species pool will virtually always co-occur, while others will rarely or never co-occur in the same habitat (McPeck 1990, Wellborn et al. 1996). Therefore, strong interactions in the food web act to focus the selective environment of constituent species into two alternative regimes (Fig. 4). Thus, although the critical role of body size in shaping both predator avoidance and competitive ability suggests that species’ phenotypes result from an evolutionary balance of these factors, strong interactions in food webs may act to either exacerbate or diminish the potential importance of competitive interactions in shaping species’ phenotypes, depending on the habitat type a species occupies.

Given these considerations, to what extent has competition-mediated selection shaped the phenotypes of the large and small species? The large species, with its large body size, high foraging rate, and high activity level, has strong competitive ability. Although it does not typically experience interspecific competition from the small species, it does co-occur with other grazers such as snails and herbivorous insects. Additionally, it

may experience strong intraspecific competition. Indeed, intraspecific competition may have a compounding effect on the evolution of larger size, with larger size causing more intense competition and, in turn, more intense selection for larger size. In fishless habitats, where large size confers a survival advantage because it provides a size refuge from predation, the large species may be relatively free to increase in size until it is constrained by other factors (e.g., Roff 1986). The small species, with its small body size, low foraging rate, and low activity level, is a comparatively poor competitor, and would likely be displaced by the large species in a direct interaction between them. Such a direct interaction between the small and large species is precluded, however, by the strong predatory interactions in the regional food web. Other potential competitors do coexist with the small species, but, at least for snails, the competitive impact is much weaker than that of the large species. Also, intraspecific competition may be less intense for the small species because of the lower per capita impact of the small species caused by its small size and low resource consumption rate. Additionally, because fish limit the abundance of the small species (Mittelbach 1988, Wellborn and Robinson 1991), the amphipods may not exist at densities great enough to cause resource limitation. Thus, despite its potential intensity, competition probably has a much weaker influence in shaping the traits of the small species than the large species. This difference between species in the fundamental structure of the trade-off between competitive ability and antipredator adaptation may have important implications for speciation in *Hyalella*. Adaptive resolution of the trade-off between competitive ability and antipredator adaptation for a species occurring in both fish and fishless habitats is likely to enhance the degree and rate of divergence between populations that exist across these habitat types, causing phenotypic diversification that may foster speciation.

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