



Relatedness and resource diversity interact to influence the intensity of competition

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When resource competition occurs between close relatives, the negative effects of competition are potentially amplified. However, kin selection theory predicts that natural selection should promote the evolution of mechanisms that minimize the intensity of competition between kin. Experimental tests of these hypotheses are mixed, however. Moreover, there is little consensus regarding the generality of either outcome, suggesting that the conditions important in determining the effects of competition between kin are likely complex and not fully understood. We performed two experiments using spadefoot toad tadpoles (*Spea multiplicata*) to evaluate the hypothesis that individuals can minimize the negative effects of exploitative competition by using alternative resources when competing with close relatives. Supporting our hypothesis, we found that only when individuals had access to alternative resources were the negative effects of competition between siblings less than between unrelated competitors. We suggest that mechanisms to lessen kin competition may be more likely to evolve in environments where alternative resources are available, and that selection to minimize exploitative competition between kin may promote the evolution of resource polyphenism. © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2013, 110, 689–695.

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INTRODUCTION

Competition for resources is an intense and pervasive agent of natural selection (Gurevitch *et al.*, 1992; Pfennig & Pfennig, 2012) and dramatically impacts multiple aspects of an individual's fitness. The negative effects of competition are potentially amplified when competition occurs between close relatives for two reasons. First, kin competition not only reduces the individual fitness of competing individuals, but also reduces their inclusive fitness through the negative effects of competition on each other (Hamilton, 1964a). Second, because resource competition is often more intense between phenotypically similar competi-

tors (Pfennig, Rice & Martin, 2007; Martin & Pfennig, 2009; Caesar, Karlsson & Forsman, 2010; Benard & Maher, 2011; Violle *et al.*, 2011), the intensity of competition itself should often be greater between close relatives than between unrelated individuals [under the assumption that the former should generally be more similar (i.e. phenotypically and ecologically) than the latter].

However, kin selection theory predicts that mechanisms should evolve to reduce kin competition when doing so maximizes inclusive fitness (i.e. the costs of altruistic behaviour directed towards kin are outweighed by the benefits [Hamilton, 1964a]). One possible strategy to minimize kin competition is to disperse away from related individuals (Lambin, Aars & Piertney, 2001). However, opportunities for dispersal are sometimes limited or absent. In these circumstances, selection may act to minimize the effects of kin competition. Indeed, some studies have found that competition between kin is less intense than competition between unrelated individuals (Jasiński, 1988;

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Brown, Brown & Wilson, 1996; Saidapur & Girish, 2001; Gerlach *et al.*, 2007); for example, via decreased interference competition (Tóth *et al.*, 2009; Lizé, Khidr & Hardy, 2012) or cooperative feeding behaviours (Hokit & Blaustein, 1997; Bazazi *et al.*, 2012). There is little consensus, however, regarding whether competition will generally be more intense between related or unrelated individuals or of the ecological conditions favouring either outcome (File, Murphy & Dudley, 2012) because other studies have found evidence that competition between kin is more intense (Shvarts & Pyastolova, 1970; Hokit & Blaustein, 1994), whereas others have failed to find an effect of relatedness on competition (Travis, 1980; Willson *et al.*, 1987; Walls & Blaustein, 1994; Smallegange & Tregenza, 2008; Twomey, Morales & Summers, 2008) or found context-dependent effects (Smith, 1990; Gramapurohit *et al.*, 2004; Caesar *et al.*, 2010). The lack of consensus among studies suggests that the conditions important in determining the affects of competition between kin are likely complex and not yet fully understood.

In the present study, we suggest that, when competing with close relatives, individuals may switch to use alternative resources and thus reduce exploitative competition with kin. Individuals that preferentially switch to an alternative, possibly less-preferred, resource when competing with kin (but not when competing with unrelated individuals) could increase their inclusive fitness. There is growing evidence that populations are often composed of individual resource use specialists that consume only a subset of a population's overall resource breadth (Bolnick *et al.*, 2003; Araújo, Bolnick & Layman, 2011). Furthermore, both field observations and experimental studies have shown that individuals can behaviourally alter their diet in response to competition (Pfennig & Murphy, 2002; Svanbäck & Bolnick, 2007; Robinson & Pfennig, 2013). Therefore, diet plasticity could be an important adaptation to minimize the effects of kin competition when alternative resources are available. This potential mechanism may have been previously overlooked because experimental studies of kin competition generally supply a single resource type, thus eliminating the possibility of reducing competition by switching to alternative resources.

We use tadpoles of the Mexican spadefoot toad, *Spea multiplicata* (Cope), to test this hypothesis. Several characteristics of *S. multiplicata* make them an excellent model system for studies of kin competition and with which to test our hypothesis. First, competition for resources among *S. multiplicata* tadpoles to grow and reach metamorphosis before the ephemeral ponds in which they develop finally dry up is often intense (Pfennig, 1990; Martin & Pfennig, 2009, 2012). Second, *S. multiplicata* tadpoles are

trophically diverse, acting as both grazers and predators, consuming microscopic detritus, algae, small crustaceans, large anostracan fairy shrimp, and other tadpoles (Pfennig, 1990; Paull, Martin & Pfennig, 2012). Third, *S. multiplicata* tadpoles discriminate related from unrelated individuals, and modify their behaviour (Pfennig, Reeve & Sherman, 1993) and development (Pfennig & Frankino, 1997; Pfennig, 1999) accordingly.

The wide resource breadth utilized by *S. multiplicata* is associated with a remarkable range of trophic phenotypes, represented by two developmentally plastic ecomorphs that comprise a resource polyphenism: an 'omnivore' morph and a 'carnivore' morph (Ledón-Rettig & Pfennig, 2011). Omnivores are generalists, and feed mostly on microscopic detritus, algae, and small crustaceans, whereas carnivores are specialists, and feed mostly on anostracan fairy shrimp (Paull *et al.*, 2012), comprising the cue that triggers carnivore development (Pfennig, 1990).

MATERIAL AND METHODS

In the present study, we investigated the effects of relatedness and resource diversity on the intensity of competition in *S. multiplicata* tadpoles. Specifically, we compared and evaluated the results from two separate experiments: (1) measuring competition between pairs of siblings and nonsiblings given a single resource type and (2) measuring competition between pairs of siblings and nonsiblings given two different resources. Comparing the effect of relatedness on competition between the two experiments allowed us to evaluate the interaction of relatedness and resource diversity on the intensity of resource competition. We predicted that the intensity of competition would not differ with relatedness when competition occurred for a single resource. By contrast, we predicted that the negative effects of competition would be more intense between nonsiblings than between siblings when competition occurred for multiple resource types.

SINGLE-RESOURCE EXPERIMENT

In spring 2004, we induced the breeding of eight male-female pairs of *S. multiplicata* [previously collected from breeding aggregations near Portal, AZ, and subsequently held at the University of North Carolina (UNC)] with subdermal injections of 0.07 mL of 0.1 mM gonadotrophin-releasing hormone and placed each pair into separate oviposition boxes filled with aged water. After oviposition, we removed the adults from each box and aerated the eggs with aquarium pumps and airstones until they developed into free-swimming larvae. We then transferred tad-

poles into new rearing tanks containing aged water, keeping the densities approximately equal across all sibships, and supplied fish food *ad libitum* (ground Wardley cichlid floating pellets).

We began the experiment 10 days after oviposition when we paired sibships based on similar larval body sizes (making four sibship pairs) and randomly selected thirty tadpoles from each sibship. We measured the wet mass of the selected tadpoles with a digital balance and assigned tadpoles to one of two treatments: (1) a sibling treatment, with two size-matched siblings, or (2) a nonsibling treatment, with two sized-matched nonsiblings. Before starting the experiment, we injected a fluorescent coloured elastomer (Northwest Marine Technology, Inc.) into the dorsal tail membrane of each tadpole: green for one of the paired tadpoles and orange for the other. We placed paired tadpoles inside plastic tanks (28 × 18 × 10 cm) filled with 6 L of aged tap water and kept in the same room maintained at 26 °C and under a 14 : 10 h light/dark cycle. We arranged the tanks in blocks of three on metal racks. The blocks consisted of a nonsibling treatment tank with tanks containing matching sibling treatment pairs on either side (one sibling pair containing tadpoles from each of the two sibships represented in the adjacent nonsibling tank). We replicated the blocks nine times for each sibship pair, for a total of 216 experimental tanks. We fed tadpoles 20 mg of ground fish food every day for 10 days (fish food simulates the detritus on which *Spea* feed in natural ponds; Pfennig, Rice & Martin, 2006). We ended the experiment after 10 days and measured each tadpole's wet mass as before, and snout–vent length (SVL) with digital calipers.

TWO-RESOURCE EXPERIMENT

In Autumn 2008, we induced the breeding of eight male–female pairs of *S. multiplicata* (previously collected from breeding aggregations near Portal, AZ, as before and subsequently held at UNC) using the methods described earlier. Five of the pairs produced clutches and we reared these sibships as described previously.

Twelve days after oviposition, we randomly assigned tadpoles from each sibship to either a focal group or a stimulus group, and then marked focal tadpoles with green elastomer and stimulus tadpoles with orange elastomer. Two days later, we measured the wet mass of the focal and stimulus tadpoles and placed each focal tadpole with a size-matched stimulus tadpole in plastic tanks (28 × 18 × 10 cm) filled with 6 L of aged tap water and kept in the same room maintained at 26 °C and under a 14 : 10 h light/dark cycle. Pairings either consisted of two tadpoles from the same sibship (sibling treatment) or a stimulus

tadpole that belonged to a different sibship from the focal tadpole (nonsibling treatment). We paired each focal sibship with every other sibship in the nonsibling treatment. For each sibship, there were 15 replicates for each treatment, for a total of 150 tanks. We placed the tanks on metal racks, alternating tanks from sibling and nonsibling treatments, and dispersed replicates from each sibship evenly across the room. Beginning 14 days after oviposition, each replicate received two resource types: 20 mg of ground fish food every other day and 20 mL of live brine shrimp (*Artemia* spp.) every day (*Artemia* are similar to the fairy shrimp on which *Spea* tadpoles feed in natural ponds). We ended the experiment after 9 days, and recorded the final wet mass, and SVL of the focal tadpoles.

STATISTICAL ANALYSIS

Our primary measure of performance in both experiments was the growth of each tadpole (i.e. the change in wet mass during the course of the experiment) in each replicate. Growth is an appropriate fitness proxy: there is a premium on rapid growth in the ephemeral ponds in which *S. multiplicata* typically breed (Pfennig, 1992) and larval body size predicts several fitness components (Pfennig *et al.*, 2007; Martin & Pfennig, 2009). Because mass can decline as tadpoles approach metamorphosis, we also used final SVL as a second measure of performance.

We first tested the hypothesis that relatedness would not affect the intensity of competition for a single resource. Accordingly, we evaluated whether growth was greater in sibling or nonsibling treatments in the single-resource experiment. We ran a linear mixed model with growth as our response variable, competitor relatedness as our fixed effect, and the random effects of block, nested within focal sibship, to account for spatial variation and variation among sibships. We fit the model using the R package 'lme4' (Bates, Maechler & Bolker, 2012), and tested our hypothesis using a Kenward–Roger Approximate *F*-test (Kenward & Roger, 1997) implemented with the R package 'afex' (Singmann, 2013). We also ran an otherwise identical model with final SVL as our response variable.

Next, we tested the hypothesis that relatedness would affect the intensity of competition for two resource types. Accordingly, we evaluated whether growth was greater in sibling or nonsibling treatments in the two-resource experiment. We ran a linear mixed model, implemented in R as described above, with growth of the focal tadpoles as our response variable, competitor relatedness as our fixed effect, and the two random effects of focal sibship and stimulus sibship, to account for variation among

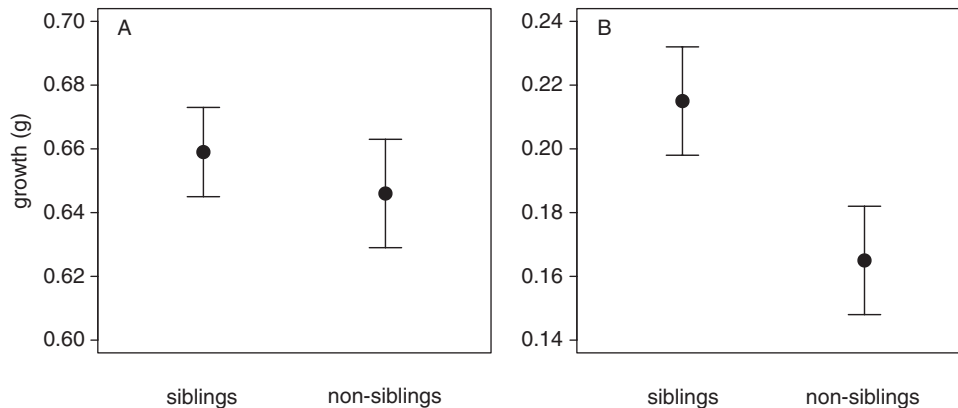


Figure 1. Growth (change in wet mass; mean \pm SE) of *Spea multiplicata* tadpoles reared with sibling or nonsibling tadpoles and supplied with one resource type (A) and focal *S. multiplicata* tadpoles reared with sibling or nonsibling tadpoles and supplied with two resource types (B).

sibships. We again ran an otherwise identical model, with final SVL as our response variable. We discarded all replicates involving tadpoles from one of the sibships in our analysis because tadpoles from this sibship had very low survival across both treatments.

Finally, we calculated Cohen's d to estimate the standardized effect size of the difference between sibling and nonsibling treatments in each experiment to compare the effect of competitor relatedness between the experiments.

RESULTS

In the single-resource experiment, we found no significant difference between sibling and nonsibling treatments in either growth ($F_{1,138.99} = 0.289$, $P = 0.591$; Fig. 1A) or final SVL (mean \pm SE): sibling = 16.89 mm \pm 0.14; nonsibling = 16.94 mm \pm 0.18, $F_{1,138.90} = 0.082$, $P = 0.775$). In the two-resource experiment, by contrast, we found that focal tadpoles achieved greater growth when competing with siblings than when competing with nonsiblings ($F_{1,93.94} = 4.135$, $P = 0.045$; Fig. 1B). Although tadpoles competing with siblings tended to achieve larger final SVL, the difference was not significant (mean \pm SE: sibling = 15.56 mm \pm 0.17; nonsibling = 15.23 mm \pm 0.2, $F_{1,94.37} = 1.548$, $P = 0.217$). By calculating standardized effect sizes for the two experiments, we found that the positive difference in growth for tadpoles competing with kin compared to unrelated tadpoles was approximately five times greater when two resources were available (Cohen's d : single-resource = 0.079, SD = 0.14; two-resources = 0.409, SD = 0.2), and approximately six times greater when measuring performance as final SVL (Cohen's d : single-resource = 0.042, SD = 0.15; two-resources = 0.25, SD = 0.1).

DISCUSSION

Generally, resource competition is expected to be most intense between the most phenotypically similar individuals (Pfennig & Pfennig, 2012). Because siblings tend to be more phenotypically similar to each other than nonsiblings, this suggests that resource competition should be especially intense between siblings. However, kin selection theory predicts that mechanisms should evolve to reduce competition between kin when doing so maximizes inclusive fitness (Hamilton, 1964a). In the present study, we set out to determine whether individuals can minimize exploitative competition with kin by exploiting alternative resources.

Using spadefoot toad tadpoles as a model system, we found that relatedness influenced the outcome of resource competition. However, as predicted, the precise effect of relatedness on competition was dependent on the availability of alternative resources. Specifically, we found that the consequences of competition did not differ between pairs of competing siblings or unrelated individuals when competition was restricted to a single resource. By contrast, the negative effects of competition were less intense for sibling pairs than for unrelated pairs when we supplied tadpoles with two different resources. These environmentally dependent results provide strong support for our hypothesis that, when competing with close relatives, individuals may preferentially use alternative resources and thus reduce exploitative competition with kin. Although tadpoles would be able to limit interference competition with siblings no matter the resource base, exploitative competition can only be minimized (without drastically impacting individual fitness by reducing food intake) by taking advantage of alternative resources.

Previous studies have demonstrated that *S. multiplicata* tadpoles can discriminate relatives from unrelated individuals (Pfennig *et al.*, 1993; Pfennig & Frankino, 1997; Pfennig, 1999) and can modify their diet in response to resource availability and competition (Pfennig & Murphy, 2002; Pfennig *et al.*, 2006). The results of the present study further suggest, however, that mechanisms to lessen kin competition may be more likely to evolve in environments where multiple resources are available and in populations that are able to exploit alternative resources and recognize kin. As noted in the Introduction, the absence of alternative resources supplied in most experimental studies of kin competition may help explain the conflicting evidence found among experiments in regards to the intensity of competition between close relatives.

An alternative, although non-mutually exclusive explanation for our results is that, by supplying two resources, we lowered the costs of altruistic behaviour by increasing the overall amount of resources available. Although we supplied only half as much ground fish food when we also supplied live *Artemia*, we did not estimate the overall calories allocated across the two experiments. However, when given two resources tadpoles grew less per day than tadpoles supplied with a single resource (Fig. 1), suggesting that the addition of a second resource in the two-resource experiment did not increase the overall amount of available energy for growth. It is also important to note that, by competing tadpoles matched for size, we may have increased the intensity of competition between pairs by increasing their mean phenotypic similarity. In addition, because our experiments were temporally separated, and differed in some details, we cannot eliminate the possibility that some other factor(s), besides resource availability, drove the differences in the effects of kin competition between them.

Competition between close relatives for resources may be an important force in the evolution of intraspecific diversity, analogous to the role of reproductive competition between close relatives in the evolution of eusociality (Hamilton, 1964b). A conspicuous example of intraspecific variation, resource polyphenism [environmentally triggered alternative resource-use phenotypes occurring within a population (such as that found in *Spea*)] is considered to evolve when interspecific competition is absent or relaxed, intraspecific competition is intense, and underutilized resources are available (Smith & Skúlason, 1996; Martin & Pfennig, 2010). We suggest that selection to escape kin competition may also promote the evolution of resource polyphenism (*sensu* Wennersten & Forsman, 2012), particularly in environments where the possibility of dispersal away from

kin is limited. Such environments would increase the costs of competition because the negative effects of competitive interactions would have a greater chance of being directed towards kin. In support of this hypothesis, resource polyphenism tends to be found in environments where dispersal opportunities are limited or absent (Pfennig & McGee, 2010; e.g. amphibian larvae inhabiting ephemeral ponds, fish inhabiting post-glacial lakes). Further studies are needed to evaluate this hypothesis.

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ARCHIVED DATA

Data deposited in the Dryad repository (Martin & Garnett, 2013).