Non-additive effects of intra- and interspecific competition between two larval salamanders

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Summary

1. Assessment of the relative strengths of intra- and interspecific competition has increased in recent years and is critical to understanding the importance of competition. Yet, whether intra- and interspecific competition can have non-additive effects has rarely been tested. The resulting fitness consequences of such non-additive interactions are important to provide the context necessary to advance our understanding of competition theory.

2. We compared the strength of additive and non-additive intra- and interspecific competition by manipulating densities of a pair of larval salamanders (*Ambystoma talpoideum* and *A. maculatum*) in experimental mesocosms within a response surface design.

3. Intraspecific density had the strongest effect on the strength of competition for both species, and few observed comparisons indicated interspecific competition was an important factor in predicting body size, growth or larval period length of either species.

4. Non-additive effects of intra- and interspecific competition influenced some response variables, including size and mass at metamorphosis in *A. maculatum*, but at a reduced strength compared to intraspecific effects alone.

5. Intraspecific competition was thus the dominant biotic interaction, but non-additive effects also impact the outcome of competition in these species, validating the importance of testing for and incorporating non-additive density effects into competition models.

Key-words: exploitative, growth rate, indirect effect, interaction modification, interference, multiplicative effect

Introduction

The outcome of competition is influenced by a number of factors, including competitor density, asymmetries in competitor ability or size, and habitat heterogeneity (Connell 1983; Persson 1985; Goldberg & Barton 1992; Gurevitch *et al.* 1992; Chesson 2000). Until relatively recently, quantifying the strength of density-dependent competitive interactions by estimating competition coefficients had been performed infrequently, despite the value this approach contributes to our knowledge of species interactions (Inouye 2001). Subsequently, quantification of competition using this method has increased for many systems, including plants (Damgaard 1998; Weigelt *et al.* 2007; Damgaard & Kjaer 2009; Damgaard & Fayolle 2010), invertebrates (Inouye 1999; Paini, Funderburk & Reitz 2008; Northfield *et al.* 2011), fishes (Young 2004; Forrester *et al.* 2006, 2010) and amphibians (Van Buskirk 2007). These studies have found both intra- and interspecific density-dependent competition to be prevalent, and often the strength of such interactions was asymmetric.

Most previous studies that quantified the strength of competitive interactions have compared the relative effects of intra- and interspecific competitor densities by assuming they are independent covariates (i.e. studies directly compare intra- and interspecific competition coefficients, but not their interaction). Non-additive effects (i.e. interaction modification; Wootton 1994) of competition also occur in many systems and are generally described as one (or more) species that modifies the outcome of interactions among two other species (e.g. Neill 1974; Morin 1995; Peacor & Werner 1997; Weigelt *et al.* 2007); in other words, non-additive effects occur between interspecific competitors. Surprisingly, few studies have tested for non-additive effects of intra- and interspecific competition (Smith-Gill & Gill 1978; Wilbur 1982; Damgaard 1998; Young 2004; Forrester *et al.* 2006), perhaps in part because of the logistical difficulties of conducting such complex experiments, and because the formulation of

most competition models do not explicitly account for non-additive effects (Billick & Case 1994; Dormann & Roxburgh 2005). Of the studies that have tested for this process, one found non-additive effects of intra- and interspecific competition to be non-significant (Damgaard 1998), two studies found that non-additive effects were substantially weaker than intraspecific effects (Young 2004; Forrester *et al.* 2006), and a fourth study revealed variable levels of significance (Smith-Gill & Gill 1978). However, Young (2004) also found that reducing *interspecific* competitive advantages via size asymmetries intensified *intraspecific* competition among juvenile salmonids because of decreased agonistic interactions among conspecifics when dominant interspecific competitors were present. Overall, these results indicate that non-additive effects of intra- and interspecific competition are infrequently tested for, appear to be reduced in strength compared to intraspecific or interspecific effects alone or are highly variable in significance. At the same time, when mechanisms of competitive asymmetry are present, such as size advantages (Persson 1985; Young 2004), a theoretical basis for non-additive intra- and interspecific competition is apparent, and testing for their importance may be critical for understanding the resulting community dynamics (Smith-Gill & Gill 1978; Morin, Lawler & Johnson 1988; Wootton 1994; Morin 1995).

We tested for non-additive effects of intra- and interspecific competition by manipulating larval densities of two pond-breeding salamanders that have known asymmetries in competitive ability using a response surface design. This approach allowed us to compare the strength of competition within and between species to the interactive effects of the two species' densities to determine the relative importance of each effect. Species interactions such as competition often play an important role in structuring pond communities (Wilbur 1997), and some support exists for non-additive interactions in this system (Wilbur 1972; Morin, Lawler & Johnson 1988; Wilbur & Fauth 1990; Wissinger & McGrady 1993). Interactions between intra- and interspecific competition are expected to be particularly relevant to amphibians due to variability in reproductive effort among years and the temporal overlap of aquatic stages that may result in fluctuating densities and size classes of larvae, which may ultimately shift the intensity of intra- and interspecific density dependence (Wilbur 1972, 1980).

Two larval salamanders ideal for testing interactions between intra- and interspecific competition are the spotted (*Ambystoma maculatum*) and mole salamander (*A. talpoideum*) because of their well-studied larval interactions and known differences in competitive ability. Both species are sympatric over much of their range with similar life histories in that adults breed in ponds in the late winter and early spring and have aquatic egg and larval stages, the latter of which compete for prey resources (Petranka 1998; Anderson 2011). Larvae of both species have been found to exhibit intraspecific density dependence, and

interspecific competition appears to be dominated by *A. talpoideum* due to their superior interference abilities (Walls & Jaeger 1987; Semlitsch & Walls 1993; Walls 1998). However, *A. maculatum* is a dominant exploitative competitor over *A. talpoideum* (Walls & Jaeger 1987; Walls 1996). Larval densities of these species are known to vary spatially and temporally throughout the larval period (T.L.Anderson, unpublished data) as *A. maculatum* metamorphoses earlier than *A. talpoideum* (Petranka 1998); thus, examination of relative density effects is ecologically relevant to this system. Previous studies on their competitive interactions (e.g. Walls & Jaeger 1987; Walls & Semlitsch 1991; Semlitsch & Walls 1993; Walls 1996; Anderson & Whiteman in press) led us to predict: (i) intraspecific density dependence for both species; (ii) asymmetric interspecific competition from *A. talpoideum* on *A. maculatum* and (iii) that non-additive effects would occur for each species. Specifically, we predicted that *A. talpoideum*'s previously observed higher rates of aggression would limit the growth and size of *A. maculatum* (sensu Young 2004).

Materials and Methods

An outdoor experimental mesocosm array was arranged in a randomized block design at Murray State University's Hancock Biological Station (HBS) in January 2010. Sixty 1000 L mesocosms (diameter = 1·7 m) were filled with aged well water, 3 kg of dry leaves (primarily *Quercus* spp. and *Carya* spp.), and inoculations of approximately 2 L of pond water collected from local ponds. Pond water additions contained concentrated zooplankton, a major constituent of larval salamander diet (Taylor *et al.* 1988) and other planktonic organisms. Tanks were not covered, which allowed natural deposition of additional prey resources, such as larvae of flying insects (e.g. dipterans, chironomids) that contributed to the overall resource base and created a reasonable facsimile pond ecosystem (Wilbur 1997). The entire array was covered by a shade cloth on 12 May that permitted 50% light transmission but still allowed natural precipitation to reach tanks.

Eggs of both salamander species that had been collected from two nearby ponds where both species are known to breed and from paired matings in the laboratory were reared in environmental chambers at HBS. Clutches from a minimum of three different females of each species were used in the experiment, and upon hatching, clutches were homogenized to equalize the contribution of genetic influences on competition. A slight asynchrony in hatching date resulted in *A. talpoideum* being added 24–48 h earlier than *A. maculatum* to each block, and blocks were added over five successive days during the first week of April. However, this asynchrony is minimal compared with natural hatching fluctuations (Petranka 1998). Total length of hatchlings was measured ($n = 50$ per species) prior to addition from digital photographs using Image J (Mott *et al.* 2010). Mean hatchling total length for *A. maculatum* was 12% longer than hatchlings of *A. talpoideum* (ANOVA; $\bar{X}_{maculatum}$ = 13·3 ± 0·014 (SE) mm, $\bar{X}_{talpoideum}$ 12·0 ± 0·001 (SE) mm; $F_{1,98} = 60·8$, $P < 0·0001$), which is similar to other studies (Walls & Altig 1986).

The response surface design consisted of 12 treatments spanning three overall densities (6, 12 and 24 total larvae, respectively) with five replicates of each treatment, totalling 60

experimental units. Three treatments contained only conspecifics for each species at each of the three overall densities. Interspecific competitor proportions were manipulated at the medium and high overall density levels with treatments of 3:1, 1:1 and 1:3 density ratios of conspecifics to heterospecifics. This resulted in density combinations of 9:3, 6:6 and 3:9 at the medium overall density and 18:6, 12:12 and 6:18 at the high density. Two tanks that contained only *A. talpoideum* (low and medium density) were not included in the analysis after salamanders were erroneously mixed between tanks, leaving four replicates of those treatments. The densities used match those observed in natural populations, both in terms of raw density and relative density between species (T. L. Anderson, unpublished data).

Once metamorphosis had begun, tanks were checked every other night for metamorphosing individuals throughout the summer and fall. Metamorphs were removed from tanks after they completely resorbed their gills, and snout-vent length (SVL), total length (TL) and mass were recorded. The tanks were drained and searched for remaining individuals after 12 months to calculate survival; some salamanders remained larval and others (*A. talpoideum* only) had become sexually reproductive, gilled adults (e.g. Patterson 1978; Semlitsch, Harris & Wilbur 1990; Whiteman 1994). We focus here on responses of metamorphs, as the effects of competition on paedomorphosis are discussed elsewhere (Anderson & Whiteman, in press).

We calculated estimates of intra- and interspecific competition coefficients, as well as the estimate for the interaction term between each species' densities using the *nls* function in R (R Development Core Team 2014). We calculated coefficients using an exponential model ($X_i = ae^{(-c(N_1 + \beta_1 N_2 + \beta_2 N_1 N_2))}$), where the parameters c, $c*\beta_1$ and $c*\beta_2$ describe the effects of intra, inter- and the non-additive effects of competition, X_i is the response of species i, and N_1 and N_2 the densities of con- and heterospecifics. This model has been used effectively in other studies of amphibian competition (Wilbur 1976, 1982; Van Buskirk 2007) and would also allow us to test for non-additive effects on body size and growth (Wootton 1994). We also tested several other competition models (see Table 1 of Inouye 2001), as well as simple linear regression to estimate the strength of competition; all provided qualitatively similar results regarding the relative strength of each type of competition to the non-additive effects.

We tested for the effects of competition for each species separately on the following response variables (based on mean values for each tank): mean SVL and mass at metamorphosis, mean larval period length, and mean overall growth (SVL at metamorphosis/days to metamorphosis). Body size at metamorphosis is often related to the fitness of amphibians and provides a measure of the likelihood of survival in the terrestrial environment (Semlitsch, Scott & Pechmann 1988; Scott 1994; Altwegg & Reyer 2003). Survival (calculated as the sum of all metamorphs and gilled individuals in each tank divided by the initial number added) was analysed using generalized linear mixed effects models using each species' density as a covariate with a binomial error distribution and tank as a random effect to correct for overdispersion (Warton & Hui 2011). We initially tested for block effects in all models, but they were not significant for any response variables and were removed. While we tested multiple response variables, and a MANOVA may be more appropriate, we are unaware of any multivariate test that would allow for an assessment of the strength of competition as was the focus of our study. The majority of the dominant effects we observed retain

significance when more stringent confidence intervals are used (99% CI), while the weaker effects drop out, further supporting our interpretation of the results (see below).

Results

On average, metamorphs were 30% larger in SVL for *A. talpoideum* compared to *A. maculatum*, but the effect varied with density. Intraspecific density had the only significant negative effects on SVL at metamorphosis for *A. talpoideum* (Table 1, Fig. 1a). The interaction term was significant for SVL of *A. maculatum*, but was only 18% the strength of conspecifics alone (Table 2, Fig. 2a). Metamorphs of *A. talpoideum* were on average more than double the mass of metamorphs of *A. maculatum*, but also varied by density treatment. The effects of competition on mass were similar to metamorph SVL, in that *A. talpoideum* exhibited significant reductions in mass at metamorphosis as conspecific density increased (Tables 1 and 2; Figs 1b and 2b). The interaction term was significant for mass at metamorphosis in *A. maculatum*, but similar to SVL, the strength of the non-additive parameter was only 20% that of the effect of conspecifics for *A. maculatum*.

In general, the larval period of *A. talpoideum* was twice as long as that of *A. maculatum*. Time to metamorphosis for *A. talpoideum* was affected nearly equally by conspecific and heterospecific density and was significant for conspecifics and nearly significant ($P = 0.051$) for heterospecific density (Table 1, Fig. 1c). This indicates overall larval density increased the number of days it took *A. talpoideum* to complete metamorphosis, but species identity did not affect this measure. For *A. maculatum*, competition did not significantly affect larval period length, but showed similar trends of higher competitor densities increasing the time to metamorphosis (Table 2, Fig. 2c).

Overall growth of metamorphs for *A. talpoideum* was significantly affected by both intra- and interspecific competition, and the strength of each type of competition was nearly identical (Table 1). Overall growth decreased as overall tank density increased (Fig. 1d). For *A. maculatum*, overall growth was predicted only by conspecific density and again growth declined as conspecific density increased (Table 2; Fig. 2d).

Survival for each species was not significantly affected by either species' density or their interaction; overall survival of *A. talpoideum* was 36% higher than *A. maculatum*; however, its mean survival was $85 \pm 15\%$ compared to $49 \pm 21\%$ SD ($\chi^2 = 13.57$ d.f. = 1, $P = 0.0002$).

Discussion

Tests for non-additive effects in competition studies are infrequent, and the majority of studies that have examined this question have focused on non-additive properties of interspecific competition among three or more species

Table 1. Summary of intra- and interspecific coefficients for mole salamanders (*Ambystoma talpoideum*) based on an exponential competition model. Bold *P*-values indicate significant coefficients. SVL is snout-vent length at metamorphosis and 'Day' is time to metamorphosis. 'Lower' and 'Upper' are the 95% confidence intervals of the parameter estimate

Response	Coefficient	Estimate	SE	*t*-value	*P*-value	Lower	Upper
SVL	Intra	**−0·00645**	**0·00306**	**−2·108**	**0·042**	**−0·01245**	**−0·00045**
	Inter	−0·00063	0·00524	−0·120	0·905	−0·01089	0·00964
	Interaction	−0·00007	0·00055	−0·128	0·899	−0·00116	0·00102
Mass	Intra	**−0·02839**	**0·01102**	**−2·575**	**0·015**	**−0·04999**	**−0·00678**
	Inter	−0·00462	0·01669	−0·277	0·784	−0·03733	0·02809
	Interaction	−0·00031	0·00192	−0·161	0·873	−0·00408	0·00346
Day	Intra	**0·01536**	**0·00554**	**2·773**	**0·009**	**0·00450**	**0·02621**
	Inter	**0·01994**	**0·00984**	**2·027**	**0·051**	**0·00066**	**0·03922**
	Interaction	−0·00095	0·00100	−0·954	0·347	−0·00290	0·00100
Overall Growth	Intra	**−0·02538**	**0·00685**	**−3·702**	**0·001**	**−0·03881**	**−0·01194**
	Inter	**−0·02449**	**0·01138**	**−2·153**	**0·039**	**−0·04678**	**−0·00219**
	Interaction	0·00122	0·00123	0·992	0·329	−0·00119	0·00364

(e.g. Neill 1974; Morin, Lawler & Johnson 1988; Dormann & Roxburgh 2005; Weigelt *et al.* 2007). Few studies have tested for an interaction between intra- and interspecific competition and have found conflicting evidence for its importance (e.g. Damgaard 1998; Young 2004; Forrester *et al.* 2006), suggesting a need for further studies investigating its relevance to explaining competitive outcomes. In our study, there was support for a significant interaction between intra- and interspecific densities for some response variables (e.g. metamorph size of *A. maculatum*). The parameter estimates of the interaction term were often much smaller than the coefficients from

intra- or interspecific effects alone, however, contrasting with our expectations. This indicates the non-additive effects were much weaker than intra- or interspecific competition, similar to the findings of Forrester *et al.* (2006). Supporting our first prediction, we found conspecific density to be the dominant effect in this study, as higher densities decreased growth and size at metamorphosis for both salamanders and lengthened the larval period for *A. talpoideum*. There was little evidence that interspecific competition by itself significantly affected responses for either species, which did not support our original prediction. In a similar mesocosm experiment, Semlitsch &
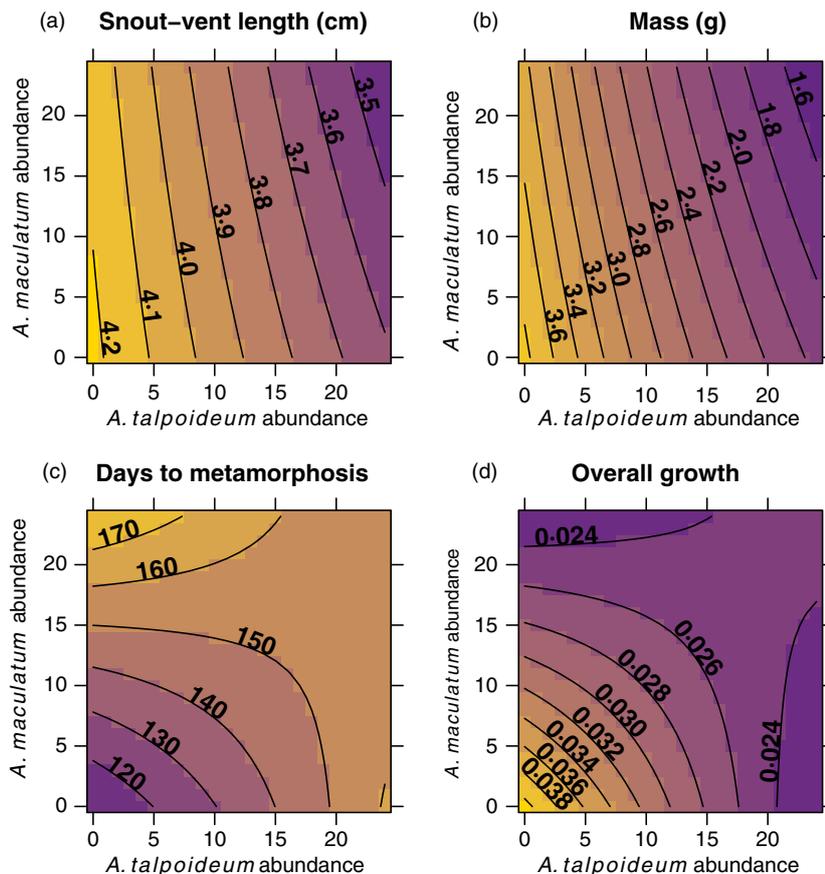

Fig. 1. Predicted responses from an exponential competition model for (a) snout-vent length (SVL) at metamorphosis, (b) mass at metamorphosis, (c) time to metamorphosis and (d) overall growth in mole salamanders (*Ambystoma talpoideum*). The *x*-axis shows the effect of intraspecific density (i.e. the focal species for each response), and the *y*-axis shows the effect of interspecific competitor density. Vertical isoclines would indicate only intraspecific competition is occurring, horizontal isoclines that only interspecific competition is occurring and diagonal (45 degree) lines would indicate that each species has equivalent effects.

Table 2. Summary of intra- and interspecific coefficients for spotted salamanders (*Ambystoma maculatum*) based on an exponential competition model. Bold *P*-values indicate significant coefficients. SVL is snout-vent length at metamorphosis and 'Day' is time to metamorphosis. 'Lower' and 'Upper' are the 95% confidence intervals of the parameter estimate

Model	Coefficient	Estimate	SE	*t*-value	*P*-value	Lower	Upper
SVL	Intra	**−0·00423**	**0·00183**	**−2·318**	**0·026**	**−0·00781**	**−0·00065**
	Inter	0·00157	0·00340	0·463	0·646	−0·00508	0·00823
	Interaction	**−0·00076**	**0·00035**	**−2·162**	**0·037**	**−0·00146**	**−0·00007**
Mass	Intra	**−0·01546**	**0·00784**	**−1·973**	**0·056**	**−0·03082**	**−0·00010**
	Inter	0·00874	0·01444	0·605	0·548	−0·01956	0·03703
	Interaction	**−0·00333**	**0·00165**	**−2·017**	**0·051**	**−0·00656**	**−0·00009**
Day	Intra	0·00523	0·00373	1·403	0·168	−0·00207	0·01253
	Inter	0·01060	0·00690	1·536	0·133	−0·00292	0·02412
	Interaction	−0·00067	0·00070	−0·951	0·347	−0·00204	0·00071
Overall growth	Intra	**−0·00999**	**0·00354**	**−2·821**	**0·007**	**−0·01692**	**−0·00305**
	Inter	−0·00990	0·00660	−1·501	0·141	−0·02283	0·00303
	Interaction	0·00002	0·00068	0·023	0·982	−0·00132	0·00135

Walls (1993) found significant but weak interspecific effects from *A. talpoideum* on *A. maculatum* in cattle tanks, consistent with our results showing intraspecific competition is the dominant effect. There is also no evidence that our results stem from geographic variation in competitive abilities, as this was shown not to affect larval interactions (Semlitsch & Walls 1993). Overall, the importance of intraspecific competition relative to interspecific competition may be a potential mechanism that permits the co-occurrence of *A. talpoideum* and *A. maculatum* in natural populations (Chesson 2000).

Both of our focal species showed higher overall growth rates, larger SVL and greater mass at metamorphosis when reared at low conspecific densities. Density-dependent regulation of body size is important, as condition at metamorphosis is often correlated with adult fitness estimates, such as fecundity and survival (Semlitsch 1985; Semlitsch, Scott & Pechmann 1988; Schmidt, Hodl & Schaub 2012; Earl & Whiteman in press). Survival was density-independent for heterospecific and conspecific densities as well as their interaction. However, as density dependence was apparent in metamorph SVL for *A. talpoideum* and *A. maculatum*, the
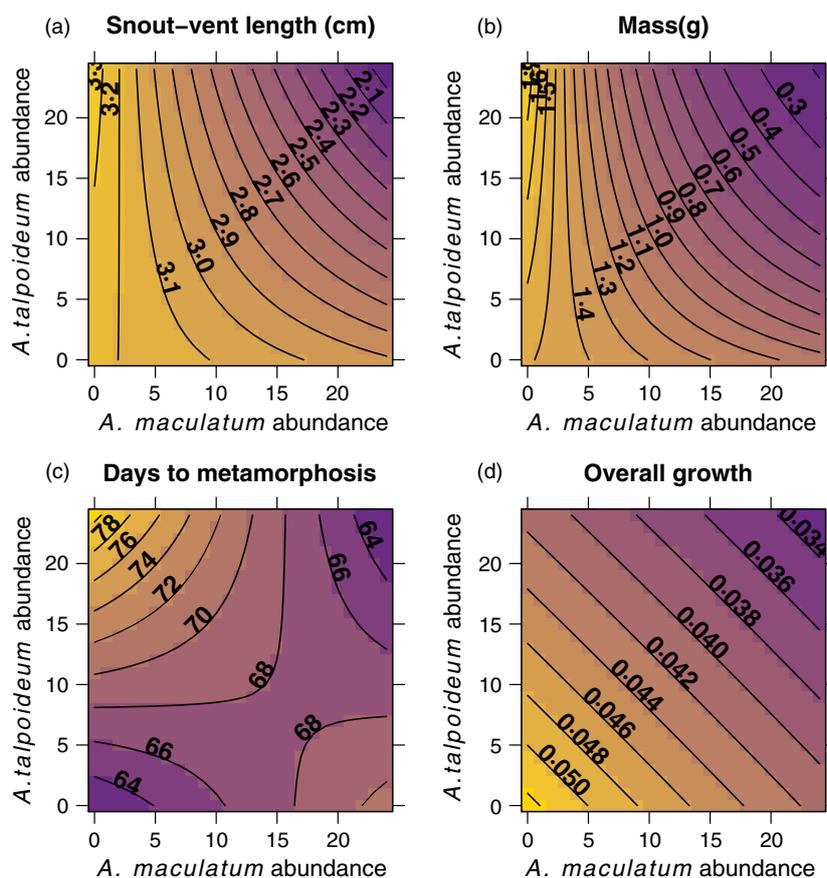

Fig. 2. Predicted responses from an exponential competition model for (a) snout-vent length (SVL) at metamorphosis, (b) mass at metamorphosis, (d) days to metamorphosis and (d) overall growth in spotted salamanders (*Ambystoma maculatum*). The *x*-axis shows the effect of intraspecific density (i.e. the focal species for each response), and the *y*-axis shows the effect of interspecific competitor density. Vertical isoclines would indicate only intraspecific competition is occurring, horizontal isoclines that only interspecific competition is occurring, and diagonal (45 degree) lines would indicate that each species has equivalent effects.

effects of larval competition may result in size-specific survival of juvenile metamorphs, which is a critical life stage for regulating population growth (Biek *et al.* 2002; Vonesh & De la Cruz 2002). Furthermore, if reduced growth rates observed in this study resulting from intraspecific effects are present in natural systems, other stressors such as predation may compound the competitive effects on size and growth that ultimately affect terrestrial survival (Gurevitch, Morrison & Hedges 2000; Chase *et al.* 2002). Survival was significantly higher for *A. talpoideum*, indicating potential dissimilarities in species' responses to unmeasured factors (i.e. experimental conditions), or that *A. talpoideum* may have a higher intrinsic rate of survival than *A. maculatum*.

The implications of non-additive effects in natural populations of these salamanders are important to consider, as both focal species show substantial spatiotemporal variability in larval density, which in some cases can be extremely high (T. L. Anderson, unpublished data). Non-additive effects from *A. talpoideum* on *A. maculatum* may become more pronounced at higher densities, increasing the overall importance of such processes that further limits size at metamorphosis, with subsequent consequences on population dynamics (Semlitsch, Scott & Pechmann 1988; Scott 1994; Earl & Whiteman, in press). Because *A. talpoideum* can overwinter in ponds (Doyle & Whiteman 2008; Anderson & Whiteman, in press), large size asymmetries may create intensive interspecific interactions among different age classes (Persson 1985; Young 2004; Van Buskirk 2007), and confer size-based competitive advantages in addition to or in concert with numerical abundance and behavioural strategies. In our system, larval *A. talpoideum* were on average 6% larger than *A. maculatum* (Anderson 2011), and metamorphosed 30% larger, which would provide advantages in interference competition over any *A. maculatum* that remained in tanks beyond their normal larval period (Walls & Jaeger 1987; Walls 1996). These size advantages may be necessary for *A. talpoideum* to succeed in the terrestrial environment, as aggression rates switch between species among metamorphic individuals (*A. maculatum* is more aggressive (Walls 1990)). Future experimental and observational investigations of density-dependent competition and non-additive effects are needed to test such hypotheses, however, which could help explain why non-additive effects of intra- and interspecific competition have received variable support.

Because the strength of non-additive effects of intra- and interspecific competition has been shown to be irregular and may be relatively small compared to intraspecific effects alone, their importance may differ by response variable (e.g. larval period versus metamorph size in this study), species or system (Smith-Gill & Gill 1978; Damgaard 1998; Young 2004; Forrester *et al.* 2006). A reasonable interpretation is therefore that non-additive effects of intra- and interspecific competition may not be an important ecological process. Yet, Young (2004) found that intraspecific competition was increased when the size of an interspecific competitor was experimentally reduced

because intensified intraspecific aggression was minimized by the larger competitor, suggesting the competitive asymmetries (in this case mediated by size) may be critical for producing non-additive effects. Similarly, asymmetries in competitive mode of the species in our study may provide an analogous mechanism as to why the non-additive effects we observed are biologically plausible: *A. talpoideum* is a dominant inference competitor, whereas *A. maculatum* is a dominant exploitative competitor (Walls & Jaeger 1987). At low density (i.e. reduced competition), *A. maculatum* can tolerate increasing levels of interspecific competition due to reduced food limitations. As conspecific density increases for *A. maculatum*, encounters with the more aggressive *A. talpoideum* would increase simultaneous to reduced food resources from intraspecific competition, resulting in a higher per capita impact on metamorph SVL and mass (i.e. curved isoclines; Fig. 2a, b). Similar effects on responses of *A. talpoideum* were not observed, perhaps due to the predominance of intraspecific interference competition in this species that overwhelmed any interspecific effects or the fact that *A. maculatum* metamorphoses earlier than *A. talpoideum*, reducing their temporal overlap. Overall, the dominant competitive mechanism within a species (size asymmetries or competitive mechanisms) may promote non-additive interactions, though at a reduced strength compared to either intra- or interspecific effects alone.

No studies have equivocally shown that that non-additive effects of intra- and interspecific competition can substantially alter the outcome of competition. However, very few studies have tested for such effects. Viewed in a more general perspective, non-additive effects, indirect effects, higher-order interactions or modifications, trait-mediated effects and others are all increasingly being recognized as significant contributors to community structure and evolutionary patterns (Billick & Case 1994; Wootton 1994; Werner & Peacor 2003; Walsh 2013). Therefore, we suggest that estimating the strength of competition while accounting for potential non-additive effects, including those between intra- and interspecific effects, is prudent to determine their ecological relevance. For some systems or interactions, these effects may be absent entirely or contribute little to explaining competitive interactions. We hypothesize non-additive intra- and interspecific competition to be of particular interest for organisms whose densities fluctuate in ways that put the relative proportions and size-structures of competitors in constant flux (and thus altering the respective relative strength of density dependence and size asymmetries of each species). Interactions of competitor densities would also be expected in situations where competitive abilities are highly asymmetric due to factors such as variability in aggressive tendencies or body size, as coexistence may be related to competitive ability more than numerical dominance (Young 2004; Van Buskirk 2007; Anderson *et al.* 2013).

Most of our understanding of competition is currently based on experimental designs and analyses that primarily

focus on the relative impacts of intra- and interspecific competition separately. When competition influences parameters associated with fitness (e.g. body size in this study), including the possibility of non-additive effects when modelling intra- and interspecific competition is thus important to explain how competitive outcomes can help predict coexistence or population growth rate. Describing the strength of non-additive effects is also valuable to determine their relative importance compared to other covariates, which may vary widely among taxa (Morin, Lawler & Johnson 1988; Inouye 2001; Young 2004; Forrester *et al.* 2006, this study). However, interpretation of non-additive effects may be difficult in some systems where behavioural research is not well developed that would provide a mechanistic basis for the interaction. Incorporating more density combinations with fewer replicates than were performed in this study may aid in interpreting non-additive effects by creating a finer-scale resolution of the response surface. Concurrent mechanistic or behavioural experiments that tie together potential causes of higher-order density interactions, such as asymmetries in ability, may then explain their role and relative importance on the impact of density-dependent competition.

Acknowledgements

Data accessibility

Data are available from the Dryad Digital Repository http://doi.org/10.5061/dryad.sb295 (Anderson 2015).

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