

# High intraguild predator density induces thinning effects on and increases temporal overlap with prey populations

Thomas L. Anderson · Raymond D. Semlitsch

Received: 1 May 2013 / Accepted: 30 October 2013 / Published online: 26 November 2013  
© The Society of Population Ecology and Springer Japan 2013

**Abstract** Intraguild (IG) predator density can alter its effects on intraguild prey populations through several mechanisms, including density-dependent processes that affect IG predator traits such as size or growth that enhance or limit its predatory abilities. We examined whether intraspecific density-dependence altered IG predator traits, as well as the subsequent interspecific effects among its intraguild prey within a larval salamander guild. Four densities of ringed salamanders (*Ambystoma annulatum*), the IG predator, were combined with the presence/absence of spotted salamanders (*A. maculatum*), the IG prey, within experimental mesocosms. We modeled the effects of *A. annulatum* density on both conspecific and heterospecific responses that would be indicative of density-dependent competition and predation, respectively. We also modeled the reciprocal interspecific effects of *A. maculatum* on *A. annulatum*. We found that increasing intraspecific density negatively affected morphological traits but not survival of *A. annulatum*. No interspecific effects of *A. maculatum* on *A. annulatum* were observed. Alternatively, traits of *A. maculatum* showed nonlinear relationships with increasing *A. annulatum* density. Thinning effects of *A. annulatum* on *A. maculatum* were observed, as survival was positively and size negatively related for *A. maculatum* with IG predator density. The temporal overlap of the IG predator and prey also increased nonlinearly with IG predator

density, intensifying the potential encounter rate of the two species. Overall, this study shows that density-dependent processes in IG predators can significantly affect traits of both themselves, as well as IG prey, which could ultimately change whether competition or predation occurs between the two groups.

**Keywords** *Ambystoma* · Competition · Predation · Priority effects · Salamander

## Introduction

Intraguild predation (IGP), where two species simultaneously compete for resources and prey upon one another, is an important ecological process across a wide diversity of organisms that has a strong theoretical basis (Polis et al. 1989; Holt and Polis 1997; Arim and Marquet 2004). Many factors influence the outcome of IGP, such as basal resource levels, the presence of alternative prey, size- or stage-structure within a population, habitat structure and the densities of the organisms involved (Mylius et al. 2001; Borer et al. 2003; Holt and Huxel 2007; Janssen et al. 2007). Variation in these factors can lead to alternative outcomes, including species coexistence, exclusion, as well as fluctuating and stochastic dynamics of the IG predator and prey.

The effects of intraguild (IG) predator density can vary in its importance depending on how and when density-dependence occurs during ontogeny. Predator aggregation (i.e., numerical responses) that occurs through different mechanisms such as changes in basal or prey resources results in greater predator densities (Mylius et al. 2001; Borer et al. 2003). These changes in density can increase predator–predator interactions (i.e., higher levels of interference competition) that limit their effectiveness in

---

**Electronic supplementary material** The online version of this article (doi:10.1007/s10144-013-0419-9) contains supplementary material, which is available to authorized users.

---

T. L. Anderson (✉) · R. D. Semlitsch  
Division of Biological Sciences,  
University of Missouri-Columbia, 110 Tucker Hall,  
Columbia, MO 65211-7400, USA  
e-mail: tlarkf@mail.missouri.edu

consuming IG prey (Sih et al. 1998). Alternatively, exclusion of IG prey can also occur through increased per capita predation rates at higher IG predator densities (Vance-Chalcraft et al. 2007). Examinations of the numerical responses often focus on fully-developed predators (Borer et al. 2003; Stier et al. 2013), or do not follow predator growth rates and/or trait changes that result from density-dependence. Similarly, experimental approaches which mimic a numerical response often use a limited range of predator densities (Wissinger 1989; Boone et al. 2002; Balfour et al. 2003), and such experiments infrequently track predator growth rates that limits the inference on how factors such as density-dependent growth can alter predators' ecological role.

In IGP systems, density-dependent processes could ultimately determine relationships between the IG predator and prey by affecting traits of each group, such as growth rates or size. For example, if the average size of the IG predators at high densities is reduced to such a degree that their ability to consume the IG prey is limited, a shift in the nature of their interactions with the putative IG prey towards a solely competitive relationship can occur. Alternatively, reduced densities of the IG predator may allow for higher growth rates, leading to larger predator sizes, and elimination of the IG prey due to enhanced foraging abilities. Direct manipulation of density-dependence, or combined manipulations of density and size that elucidate similar mechanisms, have been infrequently examined, especially in IG predators (Stenhouse et al. 1983; Burley et al. 2006). Furthermore, examinations of growing predators and prey often are focused only on examining prey growth, such as strategies that allow them to coexist with different predators, rather than the mechanisms that induce differences between traits such as gape size of the predator themselves (Urban 2007a). Understanding processes that influence predator growth patterns would thus be critical to determine patterns of coexistence and/or exclusion of interacting species (Holt and Polis 1997).

To investigate the effects of density on an IG predator, and subsequently on its IG prey, we experimentally manipulated larval densities of ringed salamanders (*Ambystoma annulatum*) in the presence/absence of an IG prey, the spotted salamander (*A. maculatum*). Larval stages of both species occur in pond habitats where IGP is a well-established (e.g., Wissinger and McGrady 1993; Davenport and Chalcraft 2012). Many organisms in these communities have immature stages that compete and/or prey upon one another due to variation in breeding phenology and the occurrence of overlapping generations; both of these processes result in size-structured populations that promote IGP (Polis et al. 1989; Wissinger 1989; Yurewicz 2004). Many of these organisms also show density-dependent

growth rates during the larval stage (Semlitsch 1987; Wissinger 1989; Wilbur 1997). For the two focal species, breeding phenology differences (fall versus spring breeding for *A. annulatum* and *A. maculatum*, respectively) influences their relative sizes when they co-occur in ponds, and both exhibit density-dependent growth (Semlitsch and Walls 1993; this study). Thus, the ability of *A. annulatum* to act as an IG predator may depend upon initial densities within a pond if it alters their growth rates and size, and ultimately determines their relationship with *A. maculatum*.

Our primary goal was to examine how density-dependent intraspecific competition in *A. annulatum* would affect conspecific traits (e.g., size at metamorphosis) and survival, as well as the same variables for sympatric *A. maculatum*. We expected larvae of *A. annulatum* reared at low initial densities to have higher growth rates, and thus greater size at metamorphosis as a result of reduced intraspecific competition. This was expected to translate into strong negative effects on *A. maculatum* traits when the two species were jointly reared. Specifically, we hypothesized reduced survival but greater growth rates and larger size at metamorphosis of *A. maculatum* due to thinning effects from the fewer, larger *A. annulatum* (Van Buskirk and Yurewicz 1998). In contrast, high initial densities of *A. annulatum* larvae were predicted to result in smaller size due to higher levels of intraspecific competition. Survival of *A. maculatum* would increase with these smaller larvae due to reduced size differences between IG predator and prey that would limit predation. Decreased growth and size of *A. maculatum* would occur, however, due to greater intra- and interspecific competition. Reciprocal negative effects from *A. maculatum* on *A. annulatum* were not expected due to the large size differences hypothesized to be present when the species were combined. Facilitation was also an alternative outcome, whereby predation on *A. maculatum* would minimize the effects of intraspecific competition within *A. annulatum* at higher densities, leading to convergent size at metamorphosis in lower density allopatric and higher density sympatric populations. We also examined whether density of the IG predator affected the degree of temporal overlap within the aquatic habitat between the two species, which can have a strong effect on species interactions (Lawler and Morin 1993).

## Methods

### Study system

*Ambystoma annulatum* is a pond-breeding salamander endemic to the Ozark Plateau in Missouri, Arkansas and Oklahoma (Petranka 1998). Adults migrate in September

through November to breed in ephemeral and permanent ponds. Larvae overwinter in ponds and undergo metamorphosis in the late spring to early summer (Hocking et al. 2008). *Ambystoma maculatum* are ubiquitous across the southeastern US, and a common prey species in studies on IGP (Stenhouse 1985; Brodman 2004; Urban 2007b). Adults of this species often breed in the late winter and early spring in ponds containing *A. annulatum*, and eggs hatch approximately 1 month before most *A. annulatum* metamorphose (T. L. Anderson, unpublished data). The larval period for *A. maculatum* lasts approximately 8–10 weeks, leading to metamorphosis that occurs from early summer into the fall. These species use similar breeding pond habitat throughout much of the range of *A. annulatum*, and often occur in sympatry (Hocking et al. 2008; T. L. Anderson, unpublished data). Thus, temporal overlap within the pond environment between larvae of these species can range from approximately a few weeks to 2 months (T. L. Anderson, unpublished data).

### Mesocosm experiment

Experimental pond mesocosms (1000 L, 1.52 m diameter; hereafter, cattle tanks), were set up in September 2011 in a circular array at a fenced outdoor research complex at the University of Missouri in Columbia, MO, USA. Tanks were filled with tap water and allowed to de-chlorinate for 5 days. Approximately 3 kg dry weight of leaves collected from Baskett Wildlife Research Area (BWRA) near Ashland, MO, USA were added to each tank (primarily *Quercus* spp., *Carya* spp. and *Acer* spp.) as a nutrient base and to provide refuge. Tanks were inoculated with concentrated zooplankton, a primary food source of larval salamanders (Taylor et al. 1988) every other day for approximately 2 weeks following collection from ponds at BWRA (approximately 3 L total volume over 2 weeks). Tanks were left open to allow for natural colonization by flying insects (e.g., chironomids and other dipterans) as an additional source of food for salamander larvae. Some potentially predaceous insects (dytiscid beetles) also colonized the open tanks but were removed as observed. Holes were drilled into the lip of each tank to permit water drainage, and water was added as needed to maintain constant water depth (~50 cm).

Late-stage embryos of *A. annulatum* were collected from Daniel Boone Conservation Area (DBCA) near Hermann, MO, USA in late September 2011 and transported to environmental chambers (held at 10 °C) at the University of Missouri. Cattle tank water was added every 3 days to the containers to acclimate the embryos/hatchlings to mesocosm conditions. Upon hatching, individuals were transferred into plastic cups filled with tank water for overnight observation to ensure viability of the hatchlings; non-viable individuals were replaced prior to addition. Hatchlings were then added

on October 13 after a 1 h acclimation period of floating the cups on the water surface within the cattle tanks. There were four experimental density treatments (8, 16, 24, and 32 hatchlings per tank) for *A. annulatum*, with six replicates of each tank. Tanks were randomly assigned both a density treatment, as well as a presence/absence treatment of *A. maculatum* (see below).

Egg masses of *A. maculatum* were collected during the first week of April 2012 from the same ponds at DBCA where *A. annulatum* collections occurred the previous fall. Egg masses were allowed to hatch, after which 24 hatchlings were added in a similar manner to *A. annulatum* on April 10, resulting in prior residence time of 181 days by *A. annulatum*. We introduced *A. maculatum* to half of the six replicates of the *A. annulatum* density treatments. The other three replicates of the *A. annulatum* density treatments served as control treatments for the tanks containing *A. maculatum*. Four control tanks with no *A. annulatum* and 24 hatchlings of *A. maculatum* were also set up at this same time but occurred over a period of 5 days due to slight hatching asynchrony. Due to several tank failures (i.e., 100 % mortality), however, replication of the *A. maculatum* addition was not equal across all *A. annulatum* densities. The resulting treatments (with replicates of *A. maculatum* presence/absence in parentheses) were: four low-density tanks (two with *A. maculatum*, two without), six medium-density (three, three), six medium–high density (three, three), and three high-density (two, one). Weekly nighttime behavioral observations that were conducted on all tanks (T. L. Anderson, unpublished data) indicated that hatchlings added to failed tanks died shortly after addition; no salamanders were ever observed in three of the failed tanks, and one tank exhibited signs of a bacterial infection that resulted in 100 % mortality (i.e., dead larvae were observed). No diseased animals were observed in any other tanks, leading us to believe the tank failures do not imply confounding mortality which affected our results. Furthermore, growth rates/sizes of *A. annulatum* match other studies, with similar model selection results (B. H. Ousterhout and R. D. Semlitsch, unpublished data). Thus, despite the loss of some experimental tanks, we feel our results accurately portray interactions between these species.

Both species were captured and measured to assess larval growth at one time point, which occurred at approximately 75 % of aquatic ontogeny (Day 154 for *A. annulatum*, Day 50 for *A. maculatum*); this measurement also provided an estimate of the size of larval *A. annulatum* at the time of *A. maculatum* addition. Captures were performed using aquarium nets at night for *A. annulatum*, and a combination of nets and mesh funnel traps for *A. maculatum*, as visibility was obscured by algae. While the goal was to capture at least three larvae in order to estimate a

mean size, three tanks for *A. annulatum* resulted in two, two, and one larvae, respectively. Captures for *A. maculatum* were less successful, as survival was very low in most tanks, often resulting in only one larval capture per tank. Measurements taken on the larvae included snout–vent length (SVL, nearest mm), total length (TL, in mm), and mass (nearest 0.01 g).

Beginning in April 2012, tanks were checked every other night for metamorphosing individuals, and continued until the end of the experiment in July, at which point 99 % of both species had completed metamorphosis. Individuals were considered metamorphs if gills were <1 mm in length, in combination with behavior indicative of leaving the tank (e.g., crawling out of the water onto the tank lip). Upon removal, metamorphs were photographed, measured for SVL, TL and mass, and euthanized.

We analyzed population (i.e., cattle tank) mean values for larval SVL (mm), overall growth rate ( $\text{mm} \times \text{day}^{-1}$ ), SVL and mass (g) at metamorphosis, days to metamorphosis and survival for each focal species. All data were tested for normality and homogeneity of variances using Shapiro and Levine's tests, respectively; no violations were found and the raw data was used thereafter. Preliminary analyses followed a similar format for each species, where we compared different mechanistic growth models using an AIC model selection approach in the R statistical program version 3.0.0 (R Development Core Team 2013). Maximum likelihood estimates of parameters for each model were calculated using the 'nls' function in R except survival. Survival of both species was modeled with a binomial error structure, and parameter estimates were calculated using the 'mle2' function from the 'bbmle' package (Bolker 2012) in R.

The results of the model selection showed that several models were equally supported for both species [see S1 and S2 in Electronic Supplementary Materials (ESM)]. For *A. annulatum*, the nonlinear models were also not clearly different from a linear model; thus, we report the results of the linear model for response variables of *A. annulatum*. For *A. maculatum*, the results showed that several nonlinear models were better supported than the linear model. We report the results of the best model for each response (see S1 and S2 in ESM). We used an ANCOVA to test for the effects of conspecific density and the presence/absence of *A. maculatum*. As survival was variable in *A. annulatum*, we used the number of *A. annulatum* metamorphs as the density in analyses of *A. maculatum*. This value likely represents the biologically-relevant predator density that *A. maculatum* experienced rather than the initial densities of *A. annulatum*. Using either density provided qualitatively similar outcomes.

We examined how the final density of *A. annulatum* affected temporal overlap of the two species by comparing

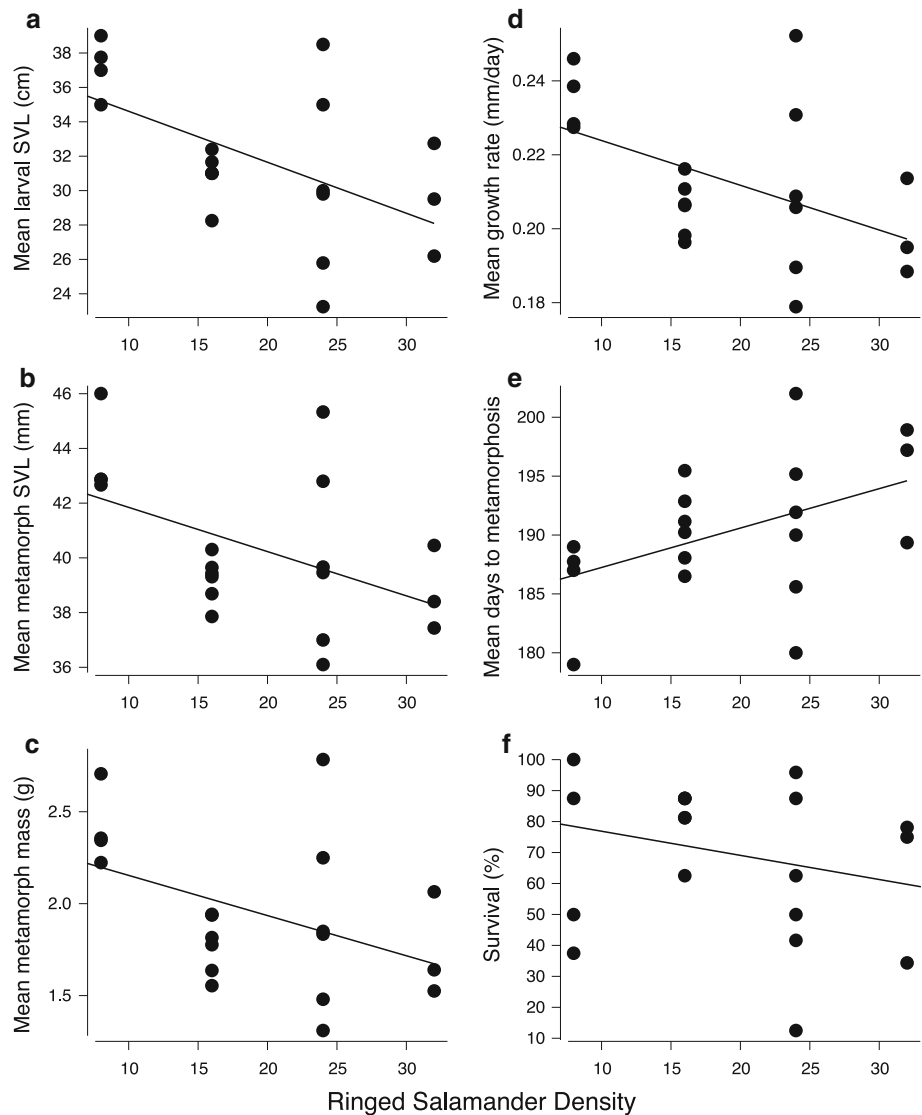
linear, three-parameter Michaelis–Menten, negative exponential, Shepherd and power law models (Bolker 2008; S1 in ESM). We calculated the minimum and maximum days of overlap which were measured as the first and last days that metamorphs of *A. annulatum* were captured, respectively, from a tank. Again, nonlinear models were clearly supported for both temporal overlap metrics, and we report the results of the top model (monomolecular function [ $y = a(1 - e^{-bx})$ ]). As nonlinear regression does not produce equivalent test statistics to linear regression, we report the  $R^2$  of the top model as an estimate of the effects of density of *A. annulatum* on *A. maculatum*, and for the relationship of temporal overlap and density (Crawley 2012).

## Results

For *A. annulatum*, the linear model and nonlinear models were equally supported, indicating that the pattern of intraspecific density-dependence was slightly nonlinear for most response variables (Fig. 1). Larval SVL for *A. annulatum* was significantly influenced by conspecific density ( $R^2 = 0.30$ ,  $t_{1,17} = -2.70$ ,  $P = 0.015$ ). Larvae of this species from the lowest density tanks were approximately 20 % larger in SVL than larvae from the three higher densities. This pattern also existed for *A. annulatum* metamorphs, where individuals from the lowest density were approximately 10 % larger in mean SVL, 26 % greater mass and had 15 % higher mean growth rates than metamorphs from the other three densities (SVL:  $R^2 = 0.19$ ,  $t_{1,17} = -2.26$ ,  $P = 0.04$ ; mass:  $R^2 = 0.14$ ,  $t_{1,17} = -2.00$ ,  $P = 0.06$ ; growth:  $R^2 = 0.19$ ,  $t_{1,17} = -2.30$ ,  $P = 0.03$ ). Individuals from the lowest density treatment completed metamorphosis on average 5 days earlier than the tanks with 16 and 24 initial densities, and 10 days earlier than the tanks with 32 individuals ( $R^2 = 0.17$ ,  $t_{1,17} = 2.17$ ,  $P = 0.04$ ). Survival of *A. annulatum* in tanks ranged from 13 to 100 % and was >60 % for most tanks; no relationship with density was apparent, however (residual deviance = 95.8,  $t_{1,17} = -1.01$ ,  $P = 0.3$ ). Linear ANCOVA models found no significant effects of *A. maculatum* presence for any response variables for *A. annulatum* (all  $P > 0.15$ ); a generalized linear model using a binomial error structure also found no effect of *A. maculatum* on survival of *A. annulatum*.

Nearly all of the most supported models for *A. maculatum* showed a saturating curve where most size and growth metrics of both larvae and metamorphs increased nonlinearly with *A. annulatum* density (see S2 in ESM; Fig. 2). In the control tanks with no *A. annulatum*, larval and metamorphic *A. maculatum* showed nonlinear patterns, and were approximately 15 % smaller in SVL ( $R^2 = 0.86$

**Fig. 1** Response variables for ringed salamanders (*Ambystoma annulatum*): larval snout–vent length (SVL) (a), metamorph SVL (b), mass (c), growth rate (d), days to metamorphosis (e), and survival (f). All points represent mean values from each cattle tank. The x-axis is the initial number of *A. annulatum*. The lines represent the predicted values from the top model of each response



and 0.74, respectively), and had 18 % slower growth rates ( $R^2 = 0.74$ ) compared with high density tanks of *A. annulatum*. The linear model was best supported for metamorph mass, and were mean values were 35 % smaller in the control tanks compared to higher density tanks ( $R^2 = 0.63$ ). Survival showed an inverse relationship, however, where survival in control tanks was 86 % higher than high density tanks. Even when *A. maculatum* were combined with the lowest density of *A. annulatum*, a strong pattern existed, where survival was three times less and size metrics were greater than 10 % compared with control tanks. Days to metamorphosis for *A. maculatum* showed no strong pattern ( $R^2 = -0.02$ ).

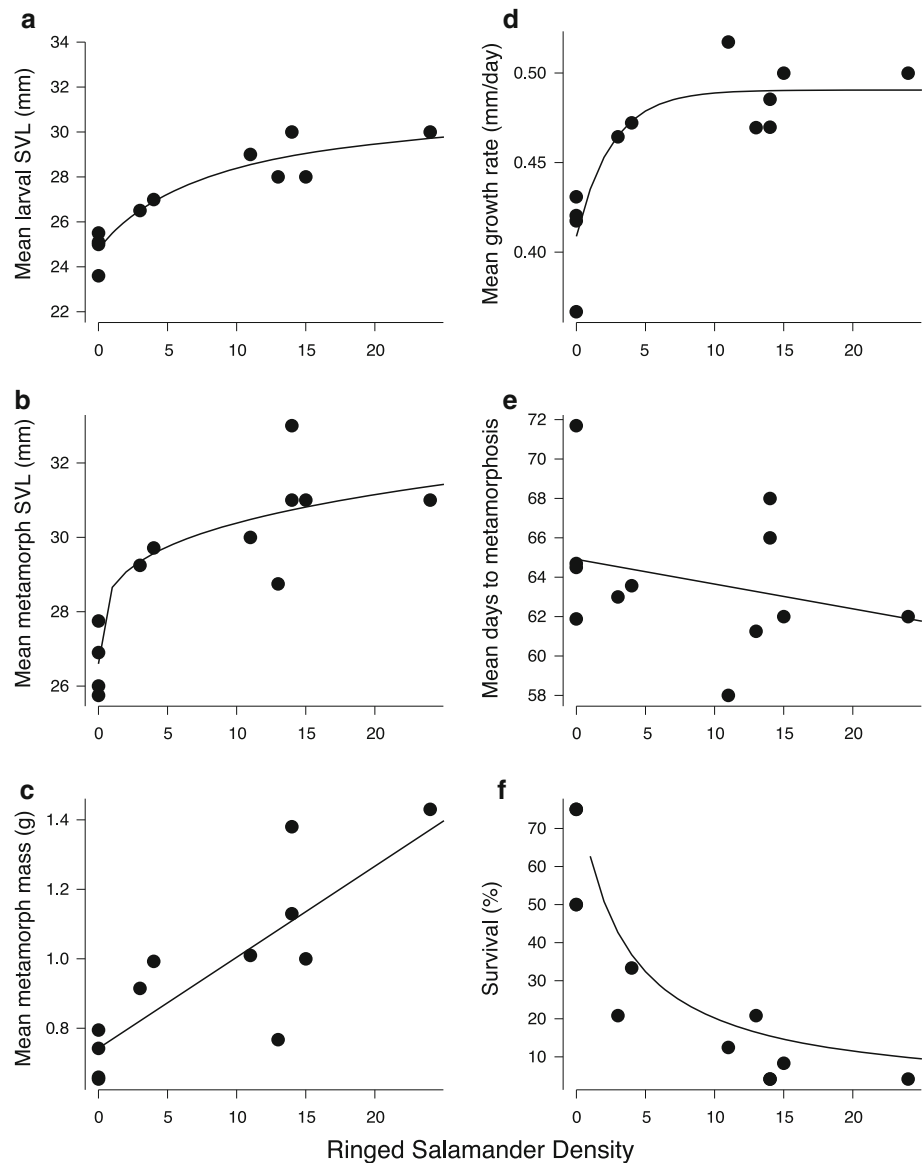
Both the maximum and minimum days of overlap within tanks had a strong saturating relationship with the density of *A. annulatum* (maximum days:  $R^2 = 0.92$ ; minimum days:  $R^2 = 0.81$ , Fig. 3). The two responses approached asymptotes at approximately 20 and 40 for minimum and

maximum days of overlap, respectively (Fig. 3), indicating a window of approximately 3 weeks that the larvae overlapped before metamorphosis started to occur for *A. annulatum*. Another 3 weeks window of overlap existed during which the density of *A. annulatum* was decreasing due to metamorphosis and extended to just prior to when *A. maculatum* started metamorphosis.

**Discussion**

Density is an important aspect of predator–prey and IGP interactions that can both limit and enhance the abilities of a predator to consume prey. We found that the density of an IG predator altered its growth rate and size but not its survival, whereas the same density-dependent processes affected both size and survival of its IG prey. These findings support the conclusion that environments that are poor

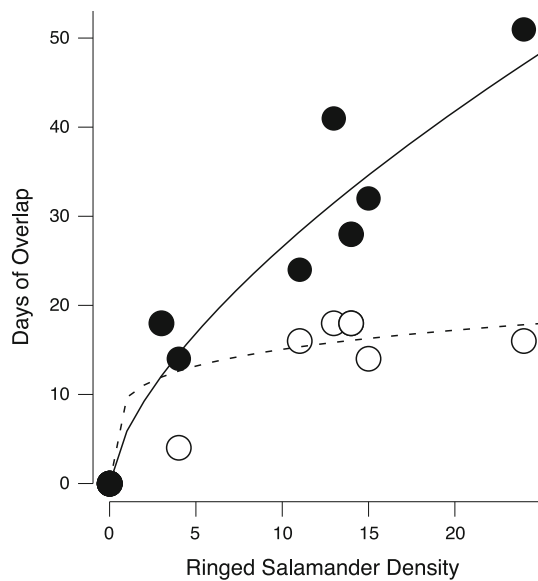
**Fig. 2** Response variables for spotted salamanders (*Ambystoma maculatum*): larval snout–vent length (SVL) (a), metamorph SVL (b), mass (c), growth rate (d), days to metamorphosis (e), and survival (f). All points represent mean values from each cattle tank. The x-axis is the number of surviving ringed salamanders (*A. annulatum*), which better represents the predator density experienced by *A. maculatum*. The zero density of *A. annulatum* is the control tanks for *A. maculatum*. The lines represent the predicted values from the top model of each response



in quality for an IG predator (i.e., higher intraspecific competition) may be significantly worse for its IG prey. In this system, the more and longer IG predators (larval *A. annulatum*) remained in the aquatic environment, the greater the effect on size and survival of its IG prey. Furthermore, many of the observed patterns also showed asymptotic relationships for the IG prey, whereby density thresholds occurred for interspecific interactions. This pattern was also reversed for the IG predator and prey, such that the IG predator, *A. annulatum*, showed a negative pattern of intraspecific density-dependence and *A. maculatum*, the IG prey, a positive saturating function with interspecific density (Figs. 1, 2). No reciprocal effects from the IG prey on the IG predator were observed, indicating the direct interactions between these species may be highly asymmetric and unidirectional. The hypothesis that consumption of *A. maculatum* would reduce the negative

effects of increased density for *A. annulatum* (i.e., convergence on similar size at metamorphosis between low and high densities when sympatric) was also not supported here.

Inverse relationships of survival and size with density were apparent (i.e., thinning effects), where both the control and the lowest density of the IG predator resulted in higher survival but a reduced size of its IG prey. Higher densities of *A. annulatum* nearly eliminated the IG prey, but the survivors were substantially larger (Fig. 2). These thinning effects are a common occurrence in intraguild and predator–prey interactions, especially among aquatic invertebrates and amphibians (Van Buskirk and Yurewicz 1998; Brodin and Johansson 2002). The resulting larger size of *A. maculatum* metamorphs from tanks that experienced thinning indicates the potential for higher juvenile survival (Scott 1990, 1994; Rothmel and Semlitsch 2006), leading us to hypothesize a



**Fig. 3** The relationship between final ringed salamander (*Ambystoma annulatum*) density and days of temporal overlap with spotted salamanders (*A. maculatum*). Maximum days of overlap (solid line, filled circles) was calculated as the last day an *A. annulatum* metamorphosed from a tank with *A. maculatum*. Minimum days of overlap (dashed line, open circles) represents when the first *A. annulatum* metamorphosed from a tank. The lines represent the predicted values from the top model of each response. The zero density of *A. annulatum* is the control tanks for *A. maculatum*

potential feedback loop between fall and spring-breeding salamanders: predation by larvae of fall-breeding species may reduce overall densities (i.e., reduced competition) of larvae of spring breeders that facilitates higher juvenile survival due to larger size at metamorphosis. While we cannot conclusively say that predation was the cause of the effects on *A. maculatum* (resource depletion by *A. annulatum* is also a potential mechanism), zooplankton were still visible in most tanks, indicating resources were not exhausted (T. L. Anderson, personal observation). Hatchlings of *A. maculatum* are palatable to *A. annulatum* larvae (T. L. Anderson, unpublished data), but their importance to, or prevalence in, the diet of *A. annulatum* is unknown. The densities that we manipulated may not have been strong enough to eliminate the potential for predation, which would be needed to examine the sole effects of competition. However, the experimental densities and sizes did match field observations of larval size distributions for the focal species (Shoop 1974; Peterson et al. 1991; Petranka 1998).

Sympatric populations of the focal species exist throughout much of the range of *A. annulatum*, but an understanding of the mechanisms that permit coexistence is lacking. Field studies of other fall-breeding salamanders (e.g., *A. opacum*) suggest that high larval densities of these IG predators affect patterns of abundance of *A. maculatum*, but their interactions alone do not exclude them from ponds

(Stenhouse 1987; Urban 2007b). Intraguild predation theory predicts that the IG prey should be superior in resource exploitation to persist with an IG predator (Holt and Polis 1997). This hypothesis has some empirical support (Morin 1999; Borer et al. 2003) but has not been tested for many systems. Larval *A. maculatum* are superior exploitative foragers as larvae over congeneric competitors (Walls 1996), but comparisons of foraging efficiency between fall and spring-breeding salamanders (i.e., IG predators and prey) have not been performed. IGP theory also predicts that basal resources must be sufficiently high for the IG predator to persist (Holt and Polis 1997; Mylius et al. 2001); in our system, either this was the case, or larval *A. annulatum* were more efficient than *A. maculatum* at consuming basal food resources. Alternatively, because the window of larval interactions is short for these two species compared to their larval period lengths, the relative consumptive abilities may be inconsequential to the outcome of their interactions; *A. maculatum* just has to survive past when metamorphosis occurs for *A. annulatum* to allow for their own metamorphosis.

Other factors may also influence their coexistence. In particular, predation on larval *A. annulatum* may reduce their densities to such a degree that the relative impacts of the few remaining larvae do not result in exclusion of *A. maculatum*. Predictions from IGP models also suggest that abundant alternative prey or increased habitat complexity may promote coexistence (Holt and Huxel 2007; Janssen et al. 2007). In ponds where high densities of *A. annulatum* occur, both of these factors may promote their coexistence with *A. maculatum*, despite density-dependent growth that would prolong their temporal overlap. Other prey sources, such as eggs and larvae of other spring-breeding amphibians, as well increased densities of invertebrate prey as the season progresses due to warmer water temperatures, provides additional food sources for *A. annulatum* which may reduce predation on *A. maculatum*. Spatial segregation within a pond by other ambystomatids suggests some partitioning of the aquatic microhabitat occurs in this guild, including the use of vegetated areas or locations of increased habitat complexity by IG prey species that would reduce encounter rates with IG predators (Brodman and Krause 2007). The effects of density on behavioral strategies such as spatial segregation are unknown, however. Other empirical studies of IGP systems have also found increased habitat complexity can reduce the incidence of IGP (Finke and Denno 2006).

An important implication from this study is when density-dependent processes occur in an IG predator, a potential switch in the type of interactions between two species (i.e., from predation to competition) can follow (Yang and Rudolf 2010). This effect may be particularly relevant in systems where priority effects occur. Density-

dependent inhibition of growth in the early-arriving species (a presumed IG predator) may negate their temporal advantage by reducing size asymmetries between species, thereby shifting the relationship from predator–prey to competition. In our study system, *A. annulatum* breeds in the fall and their larvae overwinter in ponds, providing them with a significant size advantage over hatchlings of *A. maculatum* that appear in the spring. Yet, high densities of larval *A. annulatum* may inhibit their own growth rates to such a degree that they are equally sized with their IG prey, resulting in increased competition and reduced predation effects. The intensity of species interactions may also scale to the temporal duration over which they occur, such that the influence of priority effects may matter more when the degree of overlap is greater (Yang and Rudolf 2010). When resources are exploited in temporal pulses, such as when breeding occurs in ephemeral bodies of water by invertebrates or amphibians, the degree of overlap plays an important role in the outcome of interactions (Alford 1989; Lawler and Morin 1993). Minimal overlap due to phenological mismatches or temporal segregation would reduce the effect of competition or predation and result in potentially negligible effects on the inferior/prey species (Alford 1989; Yang and Rudolf 2010), whereas longer overlap increases encounter rates, amplifying the effects of each interaction. In our study, temporal overlap ranged from 14 to 51 days, which is within the range of observed from field observations of these two species but only a portion of the potential duration as *A. annulatum* metamorphs have been observed exiting ponds as late as July (T. L. Anderson et al., unpublished data). The density of the IG predator increased this overlap at higher densities due to slower growth rates, but was shown to saturate at a density threshold (Fig. 3). When temporal overlap is greater due to higher density-dependence, increased competition between individuals of the IG prey that survive initial predation may occur.

Overall, the results of our study show that when traits such as size are affected by density, the resulting differences between individuals can determine the type and strength of species interactions that occurs. This effect is important because the cascading effects of competition and predation/IGP can result in different outcomes for both the individual species, as well as have community-level consequences (Chase et al. 2002). For species that undergo ontogenetic transitions between life stages, such as metamorphosis in amphibians and insects, this study indicates varying densities can also alter the temporal overlap of several species, which can significantly affect the outcome of their interactions (Lawler and Morin 1993). Further manipulations that vary both temporal overlap and density would reveal the relative strengths of these two mechanisms, and simultaneous manipulations of IG predator and

prey densities would be useful to understand how density-dependent processes in each species contributes to the outcome of their interactions.

**Acknowledgments** We would like to thank the Semlitsch lab for their input on study design, D. Finke, R. Holdo, M. Gompper, C. Mott and B. Ousterhout for constructive comments on an early draft of this manuscript, helpful comments from O. Kishida and two anonymous reviewers, G. Connette and B. Peterman for help in R, and L. Smith for helping collecting metamorphs. This research and TLA was funded by Department of Defense Strategic Environment Research and Development Program RC-2155. All procedures follow University of Missouri Animal Care and Use Committee protocol 7403 and eggs were collected under Missouri Department of Conservation permit 15032.

## References

- Alford RA (1989) Variation in predator phenology affects predator performance and prey community composition. *Ecology* 70:206–219
- Arim M, Marquet PA (2004) Intraguild predation: a widespread interaction related to species biology. *Ecol Lett* 7:557–564
- Balfour RA, Buddle CM, Rypstra AL, Walker SE, Marshall SD (2003) Ontogenetic shifts in competitive interactions and intraguild predation between two wolf spider species. *Ecol Entomol* 28:25–30
- Bolker BM (2008) *Ecological models and data in R*. Princeton University Press, Princeton
- Bolker BM (2012) *bbmle: Tools for general maximum likelihood estimation*. <http://CRAN.R-project.org/package=bbmle>
- Boone MD, Scott DE, Niewiarowski PH (2002) Effects of hatching time for larval ambystomatid salamanders. *Copeia* 2:511–517
- Borer ET, Briggs CJ, Murdoch WW, Swarbrick SL (2003) Testing intraguild predation theory in a field system: does numerical dominance shift along a gradient of productivity? *Ecol Lett* 6:929–935
- Brodin T, Johansson F (2002) Effects of predator-induced thinning and activity changes on life history in a damselfly. *Oecologia* 132:316–322
- Brodman R (2004) Intraguild predation on congeners affects size, aggression, and survival among *Ambystoma* salamander larvae. *J Herpetol* 38:21–26
- Brodman R, Krause HD (2007) How blue-spotted and small-mouthed salamander larvae coexist with their unisexual counterparts. *Herpetologica* 63:135–143
- Burley LA, Moyer AT, Petranka JW (2006) Density of an intraguild predator mediates feeding group size, intraguild egg predation, and intra- and interspecific competition. *Oecologia* 148:641–649
- Chase JM, Abrams PA, Grover JP, Diehl S, Chesson P, Holt RD, Richards SA, Nisbet RM, Case TJ (2002) The interaction between predation and competition: a review and synthesis. *Ecol Lett* 5:302–315
- Crawley MJ (2012) *The R book*. Wiley, West Sussex
- Davenport JM, Chalcraft DR (2012) Evaluating the effects of trophic complexity on a keystone predator by disassembling a partial intraguild predation food web. *J Anim Ecol* 81:242–250
- Finke DL, Denno RF (2006) Spatial refuge from intraguild predation: implications for prey suppression and trophic cascades. *Oecologia* 149:265–275
- Hocking DJ, Rittenhouse TA, Rothermel BB, Johnson JR, Connor CA, Harper EB, Semlitsch RD (2008) Breeding and recruitment



- phenology of amphibians in Missouri oak-hickory forests. *Am Midl Nat* 160:41–60
- Holt RD, Huxel GR (2007) Alternative prey and the dynamics of intraguild predation: theoretical perspectives. *Ecology* 88:2706–2712
- Holt RD, Polis GA (1997) A theoretical framework for intraguild predation. *Am Nat* 149:745–764
- Janssen A, Sabelis MW, Magalhães S, Montserrat M, van der Hammen T (2007) Habitat structure affects intraguild predation. *Ecology* 88:2713–2719
- Lawler SP, Morin PJ (1993) Temporal overlap, competition, and priority effects in larval anurans. *Ecology* 74:174–182
- Morin P (1999) Productivity, intraguild predation, and population dynamics in experimental food webs. *Ecology* 80:752–760
- Mylius SD, Klumpers K, de Roos AW, Persson L (2001) Impact of intraguild predation and stage structure on simple communities along a productivity gradient. *Am Nat* 158:259–276
- Peterson CL, Wilkinson RF, Moll D, Holder T (1991) Premetamorphic survival of *Ambystoma annulatum*. *Herpetologica* 47:96–100
- Petranka JW (1998) Salamanders of the United States and Canada. Smithsonian Institution Press, Washington [D.C.]
- Polis GA, Myers CA, Holt RD (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annu Rev Ecol Syst* 20:297–330
- R Development Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org/>
- Rothermel B, Semlitsch R (2006) Consequences of forest fragmentation for juvenile survival in spotted (*Ambystoma maculatum*) and marbled (*Ambystoma opacum*) salamanders. *Can J Zool* 84:797–807
- Scott DE (1990) Effects of larval density in *Ambystoma opacum*: an experiment in large-scale field enclosures. *Ecology* 71:296–306
- Scott DE (1994) The effect of larval density on adult demographic traits in *Ambystoma opacum*. *Ecology* 75:1383–1396
- Semlitsch RD (1987) Density-dependent growth and fecundity in the paedomorphic salamander *Ambystoma talpoideum*. *Ecology* 68:1003–1008
- Semlitsch RD, Walls SC (1993) Competition in two species of larval salamanders: a test of geographic variation in competitive ability. *Copeia* 1993:587–595
- Shoop CR (1974) Yearly variation in larval survival of *Ambystoma maculatum*. *Ecology* 55:440–444
- Sih A, Englund G, Wooster D (1998) Emergent impacts of multiple predators on prey. *Trends Ecol Evol* 13:350–355
- Stenhouse SL (1985) Interdemic variation in predation on salamander larvae. *Ecology* 66:1706–1717
- Stenhouse SL (1987) Embryo mortality and recruitment of juveniles of *Ambystoma maculatum* and *Ambystoma opacum* in North Carolina. *Herpetologica* 43:496–501
- Stenhouse SL, Hairston NG, Cobey AE (1983) Predation and competition in *Ambystoma* larvae: field and laboratory experiments. *J Herpetol* 17:210–220
- Stier AC, Geange SW, Bolker BM (2013) Predator density and competition modify the benefits of group formation in a shoaling reef fish. *Oikos* 122:171–178
- Taylor BE, Estes RA, Pechmann JHK, Semlitsch RD (1988) Trophic relations in a temporary pond: larval salamanders and their microinvertebrate prey. *Can J Zool* 66:2191–2198
- Urban MC (2007a) The growth-predation risk trade-off under a growing gape-limited predation threat. *Ecology* 88:2587–2597
- Urban MC (2007b) Predator size and phenology shape prey survival in temporary ponds. *Oecologia* 154:571–580
- Van Buskirk J, Yurewicz KL (1998) Effects of predators on prey growth rate: relative contributions of thinning and reduced activity. *Oikos* 82:20–28
- Vance-Chalcraft HD, Rosenheim JA, Vonesh JR, Osenberg CW, Sih A (2007) The influence of intraguild predation on prey suppression and prey release: a meta-analysis. *Ecology* 88:2689–2696
- Walls SC (1996) Differences in foraging behaviour explain interspecific growth inhibition in competing salamanders. *Anim Behav* 52:1157–1162
- Wilbur HM (1997) Experimental ecology of food webs: complex systems in temporary ponds. *Ecology* 78:2279–2302
- Wissinger SA (1989) Seasonal variation in the intensity of competition and predation among dragonfly larvae. *Ecology* 70:1017–1027
- Wissinger S, McGrady J (1993) Intraguild predation and competition between larval dragonflies: direct and indirect effects on shared prey. *Ecology* 74:207–218
- Yang LH, Rudolf VH (2010) Phenology, ontogeny and the effects of climate change on the timing of species interactions. *Ecol Lett* 13:1–10
- Yurewicz KL (2004) A growth/mortality trade-off in larval salamanders and the coexistence of intraguild predators and prey. *Oecologia* 138:102–111