Top predators and habitat complexity alter an intraguild predation module in pond communities

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Summary

1. Predator diversity and habitat complexity frequently influence species interactions at lower trophic levels, yet their joint investigation has been performed infrequently despite the demonstrated importance of each individual factor.

2. We investigated how different top predators and varying habitat complexity influence the function of an intraguild predation module consisting of two larval salamanders, intraguild predator *Ambystoma annulatum* and intraguild prey *A. maculatum*.

3. We manipulated predator food webs and habitat complexity in outdoor mesocosms.

4. Top predators significantly influenced body condition and survival of *A. annulatum*, but habitat complexity had minimal effects on either response.

5. A three-way interaction among the covariates top predator identity, habitat complexity and *A. annulatum* survival influenced body condition and survival of *A. maculatum* via a density-mediated indirect effect. Different top predator combinations had variable effects in different habitat complexity treatments on intraguild predator (*A. annulatum*) survival that subsequently influenced intraguild prey (*A. maculatum*) body condition and survival.

6. Future work should consider how different top predators influence other food web components, which should vary due to predator attributes and the physical environments in which they co-occur.

Key-words: *Ambystoma*, amphibian, competition, density-mediated effect, mosquitofish, salamander

Introduction

Community structure is simultaneously determined by both biotic and abiotic factors (Morin 2011). Food web composition or diversity, traits of each organism and their relative abundances can all alter species interactions, which altogether are simultaneously influenced by habitat heterogeneity or complexity. These synergistic components of communities result in highly complex systems that are often difficult to interpret, as they contain direct and indirect effects, feedback loops and other context-dependent associations (Werner & Peacor 2003; Agrawal *et al.* 2007). Yet, teasing apart the complexity of such systems is a priority, as nuanced and synergistic processes concurrently affect population dynamics, species interactions and community structure. Here, we test how predator food web complexity and habitat heterogeneity simultaneously influence intraguild predation.

Intraguild predation (IGP) is a widespread interaction that occurs in many ecosystems (Arim & Marquet 2004) that can strongly influence population dynamics and community structure (Polis, Myers & Holt 1989; Polis & Holt 1992; Holt & Polis 1997). IGP is most commonly depicted as a simplified food web (i.e. module) composed of three nodes: an intraguild (IG) predator, an IG prey and their shared basal resource. In addition to competing for resources, the IG predator and IG prey also can prey upon one another (Holt & Polis 1997). Examinations of simplified food webs such as IGP modules have been useful to understand the importance of species interactions. However, reducing complex ecological communities to two- or three-way interactions may not capture important underlying processes that alter their outcomes. These underlying factors can stem from within an IGP module, such as the amount of basal resources (Borer *et al.* 2003), or from size and age structure of the predator and/or prey populations (Mylius *et al.* 2001). IGP modules can also be affected by external factors, such as habitat or food web complexity (e.g. Finke & Denno 2002, 2004). When

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food webs consist of multiple predator species, simultaneously competing with and preying upon one another (i.e. multispecies IGP; Holt & Huxel 2007), further complications can arise in attempting to understand predator population dynamics, as different species can have both direct and indirect effects on each other as well their shared prey. Although examination of diverse predator communities is more difficult due to the myriad of connections among species, understanding of these systems is critical given the importance of predator identity and diversity to overall trophic dynamics (McPeek 1998; Finke & Denno 2004; Schmitz 2007).

In addition to biotic factors, the physical landscape can further alter the functioning and outcome of IGP modules. In particular, increased habitat complexity can mediate the effect of predators by limiting visibility of prey to predators, altering attack rates of predators and providing refuge that predators cannot navigate into (Swisher, Soluk & Wahl 1998; Finke & Denno 2002; Warfe & Barmuta 2006; Hossie & Murray 2010). Alternatively, when different predators exhibit complementary hunting strategies, prey can be driven from refuges (or habitat types), increasing their susceptibility to other predators in a different habitat (Huang & Sih 1990; Soluk 1993; Losey & Denno 1998; Carey & Wahl 2010). The effect of habitat complexity also varies in its impacts on the outcome of IGP and depends on traits of both the predators and prey. Because of this, predicting the impact of habitat complexity on IGP is difficult. Furthermore, few studies have evaluated the overall importance of habitat complexity, predator food web complexity and their synergistic effects (e.g. Finke & Denno 2006; Grabowski, Hughes & Kimbro 2008). Such studies are needed to synthesize the effects of habitat complexity on IGP and overall community structure.

Intraguild predation in pond communities is largely driven by size-mediated priority effects, whereby early-arriving species attain larger sizes over later-arriving species, which provides them predatory and competitive advantages (Rasmussen, Van Allen & Rudolf 2014). This type of priority effect occurs for many organisms that utilize pond habitats, including larval amphibians (e.g. ambystomatid salamander larvae) and holometabolous insects (e.g. dragonfly naiads) (Wissinger 1989; Padeffke & Suhling 2003; Segev & Blaustein 2007; Urban 2007; Anderson & Semlitsch 2014). Initial ontogenetic stages of both early-arriving (i.e. the IG predator) and later-arriving (the IG prey) species are subject to predation by a wide diversity (and in some cases extremely high densities) of vertebrate and invertebrate predators (Urban 2007). Individuals of the early-arriving species that escape predation transition into size classes impervious to gape-limited predators, and can exist as IG predators (or top predators) and superior competitors to later-arriving species due to size advantages gained during ontogeny (Mylius *et al.* 2001; Miller & Rudolf 2011; Rasmussen, Van Allen

& Rudolf 2014). Therefore, the factors that influence the number of IG predators that survive, and the size of each individual relative to their IG prey, are critical to determining the outcome of IGP. Furthermore, the relative size of the IG predator to IG prey influences the type of interaction that occurs, where smaller size classes of IG predators may primarily compete with their IG prey and larger size classes primarily interact with smaller size classes as predator and prey (Hin *et al.* 2011). As predation limits survival and often alters growth rates of prey, top predator identity, diversity and abundance would be expected to influence this link between IG predator and prey, but has infrequently been investigated (Wissinger *et al.* 1999). Habitat features also frequently influence predation in pond communities by altering attack rates, as well as providing refuges for prey species (Babbitt & Tanner 1998; Baber & Babbitt 2004; Hossie & Murray 2010). The simultaneous effects of predator food web composition and habitat complexity on IGP modules have only been infrequently investigated in pond systems.

We tested whether the presence of different top predators and increasing habitat complexity influenced the outcome of an intraguild predation module within experimental pond food webs (Fig. 1). Specifically, we tested whether different combinations of three top predators in pond food webs that varied in life-history traits influenced an IGP module among larval stages of two species of salamanders. We expected survival and body size of each salamander species to vary by predator combination due to gape limitations, hunting strategies and the presence/absence of habitat complexity.

Materials and methods

STUDY SYSTEM

Our experimental food webs consisted of up to five species that commonly co-occur in ponds in Missouri, USA (Shulse *et al.* 2010; Peterman *et al.* 2014): ringed salamanders (*Ambystoma annulatum*) and spotted salamanders (*A. maculatum*), the central newt (*Notophthalmus viridescens louisianensis*), aeshnid dragonfly nymphs (*Anax* spp.) and adult mosquitofish (*Gambusia holbrooki*; Fig. 1). Larval stages of the two salamanders form an IGP module because of differences in breeding phenology (*A. annulatum* = fall-breeder and IG predator; *A. maculatum* = spring-breeder and IG prey) that lead to larval size asymmetries that permits predation (Anderson & Semlitsch 2014). High larval densities of *A. annulatum* positively affect body size and negatively affect survival of *A. maculatum* (Anderson & Semlitsch 2014), but individual *A. annulatum* are limited in their attack rates if size disparities with *A. maculatum* are reduced (Thomas L. Anderson, unpublished data), creating the expectation that the IGP module would be altered if top predators influenced either growth or survival of *A. annulatum*.

Because the top predators exhibit variable hunting strategies and have different gape limitations, alteration to IGP between salamanders should vary based on the top predator present. Newts are visually oriented, active foragers that search through dense vegetation and leaf litter for prey items (Petranka 1998).
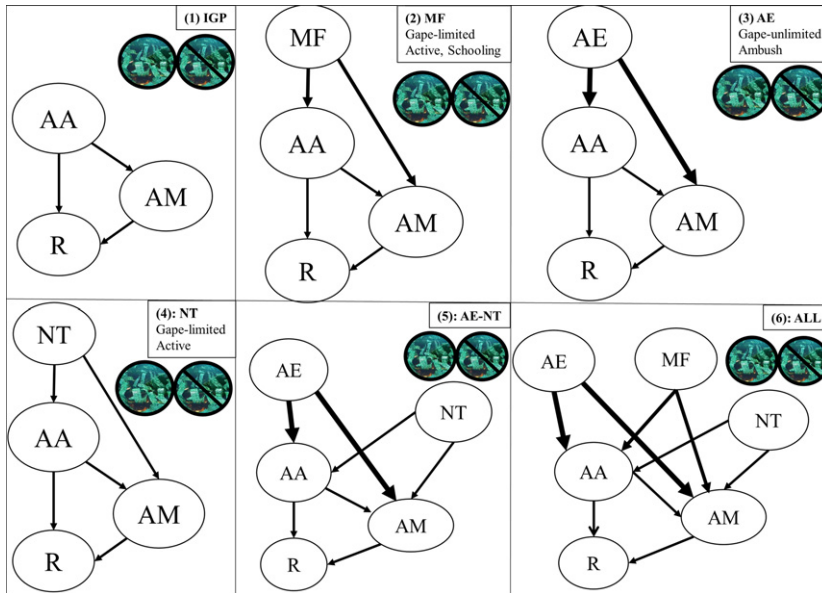
Fig. 1. Diagram of basic IGP module of two larval salamanders (1) combined with different top predator treatments (2–6). All food webs were crossed with the presence (filled circle) or absence (filled circle with crossbar) of habitat complexity. Open circles represent ringed salamanders, *Ambystoma annulatum* (AA), and spotted salamanders, *A. maculatum* (AM), late instar dragonfly nymphs, Aeshnidae (AE), adult Central newts, *Notophthalmus v. louisianensis* (NT), mosquitofish, *Gambusia holbrooki* (MF). The basal resource (R) was not manipulated. Text under treatment names indicates predator gape type and hunting strategy. Thickness of arrows indicates the predicted relative effects of each predator.

Mosquitofish are an introduced species of top minnow that actively forages in open water as well as in dense vegetation (Baber & Babbitt 2004), and often have substantial effects on amphibian recruitment (Segev, Mangel & Blaustein 2009; Shulse *et al.* 2012; Shulse & Semlitsch 2013). In contrast, aeshnid dragonfly naiads are voracious predators of larval amphibians that use ambush tactics (i.e. sit-and-pursue; Preisser, Orrock & Schmitz 2007). All three top predators can consume hatchlings of both species (Walters 1975; Drake *et al.* 2014). However, mosquitofish and newts are both gape-limited, and salamander larvae quickly grow into size classes invulnerable to consumption (Urban 2007; Shulse & Semlitsch 2013). Dragonfly nymphs are less gape-limited and can consume large amphibian larvae, meaning ambystomatid larvae are susceptible throughout their aquatic ontogeny (Caldwell, Thorp & Jervey 1980).

Based on these life-history traits, we expected the gape-unlimited dragonflies would have the greatest impact on both salamanders, followed by the gape-limited mosquitofish and adult newts (Preisser, Orrock & Schmitz 2007; Davenport, Hossack & Lowe 2014). We also expected predation by larval dragonflies, a sit-and-pursue predator, would be heightened in more structurally complex habitats than the active predators (mosquitofish and newts) (Preisser, Orrock & Schmitz 2007; Orrock *et al.* 2013). If the top predators influenced the IG predator (*A. annulatum*), we expected cascading effects would ensue for the IG prey (*A. maculatum*). When all three predators were present, we expected the greatest overall negative effects as all microhabitats (cover and open water) would be occupied by the different predators. Finally, we only focus on the direct consumptive effects of top predators on the larval salamanders, though we recognize interspecific competition for zooplankton or other invertebrates, as well as non-consumptive effects (i.e. behavioural shifts), likely occur among predators and with both salamander species (Davenport, Hossack & Lowe 2014).

EXPERIMENTAL SET-UP

We conducted the experiment in 1000-L outdoor mesocosms (hereafter, tanks) from October 2012 to July 2013. Tanks were arranged in a rectangular array within a fenced enclosure at the University of Missouri, Columbia, MO, USA. We completely filled tanks with tap water on 6 September 2012 and allowed them to de-chlorinate for approximately 2 weeks. We added 2·5 kg of dry leaves to each tank that were collected from Baskett Wildlife Area near Ashland, MO, on 21 September. Concentrated zooplankton additions collected from nearby wildlife ponds began on 25 September and continued until the start of the experiment, totalling approximately 3 L in volume per tank. We initially covered tanks with window screen covers to prevent colonization by predaceous insects, but were removed at the initiation of the experiment as many of these predators were entering dormancy. Libellulid dragonflies did colonize tanks in the last few weeks of the experiment, but none reached a size that would allow them to prey upon the remaining larval salamanders.

We collected eggs of *A. annulatum* from two pond basins at Fort Leonard Wood (FLW), MO, in late October 2012 and brought them back to finish development in indoor environmental chambers near the mesocosm array. We added hatchlings (*n* = 32 individuals) to each tank on 4 November. We collected eggs of *A. maculatum* in early April 2013 from the same locations at FLW where *A. annulatum* collections had occurred. We added 24 hatchlings of *A. maculatum* split across two separate addition dates (12 hatchlings on 24 and 29 April) due to hatching asynchronies. Densities of both species matched those found in natural populations (Thomas L. Anderson, unpublished data).

We collected predators from several ponds at FLW on 3 November 2012. They were transported back to the University of Missouri and stored in a controlled temperature room at approximately 10 °C prior to adding to tanks on 10 November. We collected predators of approximately equal size within each group. Mean total length of mosquitofish was 38·9 ± 5·18 SD mm. For newts, we tried to collect only immature or male adult newts [mean ± SD snout-vent length (SVL) = 36·5 ± 2·4 mm; mean ± SD head width (HW) = 7·2 ± 0·4 mm]. We did not identify aeshnids below genus, assuming functional equivalency between species. Because dragonflies were of approximately equal size (ca. 5th instar), we expected behavioural interference among the naiads, but did not expect predation between dragonflies; we also did not expect them to physically interact with newts or mosquitofish. Due to the duration of the experiment, reproduction by newts and mosquitofish occurred

in some tanks during the last few weeks of the experiment. Nearly all of *A. annulatum* and the majority of *A. maculatum* had metamorphosed by this point, however, suggesting these additional animals likely had minimal effects on the outcome of the experiment.

We manipulated habitat complexity within tanks by randomly assigning vertical structure treatments to half of all predator treatment replicates on 1 November (Fig. A1 in Appendix S1, Supporting information). Structure consisted of strips of 70% shade cloth (ca. 50 × 5 cm, PAK Unlimited, Cornelia, GA) that were glued along the entire length of five separate pieces of polyvinyl chloride (PVC) pipe (lengths of 35, 41, 49, 55 and 58 cm). We added the five pieces of PVC parallel to each other to the south side of each tank, spaced about 20 cm apart, with the longest piece spanning the centre of the tank. The shade cloth was sufficiently buoyant to remain vertical (perpendicular to the water surface) throughout the course of the experiment and would be analogous to cattails in natural ponds in both structure and density. Thus, our habitat complexity treatments were absent (leaves only) and present (leaves + vertical cover).

Our design included twelve total experimental treatments with four replicates per treatment (Fig. 1). These treatments included six food webs that were then crossed with the presence/absence of vertical cover. The six food webs included a simple IGP module consisting of only larval salamanders and no top predators, the IGP module + mosquitofish only ($n = 3$ individuals), the IGP module + newts only ($n = 2$ individuals), the IGP module + aeshnids only ($n = 4$ individuals), the IGP module + aeshnids + newts and the IGP module + all three predators (Fig. 1). We did not have all possible combinations of predators because of the logistical difficulties in setting up that many mesocosms; therefore, our results are somewhat limited on how multiple top predators affect IGP. The densities of predators we used are low relative to some natural populations, but given that we were interested in the effects of lethal predation, the low densities were expected to permit survival of at least some ambystomatids. Our predator treatments were additive in nature for the combinations that involved more than one species (i.e. overall density of predators was not held constant).

If dead and/or sick looking predators were observed, we replaced them with similarly sized individuals collected from a nearby pond to maintain a constant density until metamorphosis had begun for *A. annulatum* (20 May 2013). The number of predators replaced was relatively low ($n = 6$ newts, $n = 3$ aeshnids), and primarily occurred due to overwintering mortality. While replacement of predators stopped once *A. annulatum* began to undergo metamorphosis, the presence of exuvia and/or dead nymphs that unsuccessfully metamorphosed was recorded to estimate the length of time that aeshnids overlapped with both salamander species. While this would impose a different predation regime on *A. maculatum* (i.e. a shorter length of time with aeshnids), it matches the natural phenology of pond food webs. All mosquitofish and newts were recovered from tanks at the end of the experiment.

We monitored larval *A. annulatum* growth by capturing larvae at night at two time points during the spring (ca. 6 April and 22 April). We captured up to five larvae per tank, and salamanders were dorsally photographed in a plastic tray filled with water over a ruler. We then measured approximate snout-vent length (SVL) by measuring to the distal junction of the hind limbs to the body using IMAGEJ (Rasband 1997).

Beginning in May 2013, we checked tanks for metamorphosing individuals at least every other night. We removed salamanders that had completely reabsorbed gills from tanks and recorded SVL, total length and mass (in grams) measurements, as well as the date. Size at metamorphosis is correlated to adult fecundity, fitness and survival in amphibians (Semlitsch, Scott & Pechmann 1988; Scott 1994) and thus is important to assess as a proxy for predation effects on population dynamics. We scored metamorphs for injury in four categories: (i) missing tail tip, (ii) missing limb, (iii) missing majority of tail and (iv) missing multiple body parts (Semlitsch & Reichling 1989). We terminated the experiment the second week of July after >90% of salamanders had completed metamorphosis, drained the tanks and carefully searched the leaf litter to recover any remaining salamanders and predators.

ANALYSIS

We analysed body condition at metamorphosis and larval period length for both *A. annulatum* and *A. maculatum* using linear mixed models in the *lme4* package within R (Bates, Maechler & Bolker 2013; R Development Core Team 2014). Body condition was calculated by dividing mass by SVL ($g*cm^{-1}$). Individual salamanders were used as data points with tank as a random effect in all mixed models to account for non-independence of the response variables. We analysed survival of both species with generalized linear models using a quasibinomial error structure to account for overdispersion. We calculated survival as the number of metamorphs and larvae successfully recovered from tanks when the experiment was terminated. The majority of *A. annulatum* had completed metamorphosis (99%), whereas a greater number of *A. maculatum* remained larval (75% had undergone metamorphosis). Therefore, for *A. maculatum,* we separately analysed overall survival (larvae + metamorphs), the number that underwent metamorphosis and the number that remained larval in each treatment. We analysed metamorph injury for *A. annulatum* using a two-column matrix response variable (number injured, number uninjured) with a generalized linear model and a quasibinomial error distribution; predator treatment, cover treatment and their interaction were predictive factors. Few injuries were observed on metamorphs of *A. maculatum*, leading us to not statistically analyse this species.

In all models for both species, we tested for the main effects of predator treatment, cover and their interaction. For *A. maculatum*, we also added the survival of *A. annulatum* as an additional covariate, including all two- and three-way interaction terms. We retained interaction terms at marginally significant *P*-values ($P < 0.1$) as they contributed meaningful variation to the outcome, but dropped the three-way interaction if $P > 0.1$. We always included the habitat and predator treatment interaction term, as that was our original experimental design. Tukey's HSD post hoc tests were performed to examine treatment differences using the '*lsmeans*' package in R (Hothorn, Bretz & Westfall 2008). The survival of *A. annulatum* was also included to understand if the responses of *A. maculatum* were the result of indirect effects from top predators influencing *A. annulatum*. If the three-way interaction was significant, this would indicate that predators directly affected *A. annulatum*, and this effect varied by habitat treatment, which resulted in differential effects on *A. maculatum*.

Finally, we tested whether predators and cover influenced the growth rate of larval *A. annulatum* to understand whether the

predators altered the size ratio between larval *A. annulatum* and hatchling *A. maculatum*. We used larval SVL from 22 April as our response variable, as this was the approximate date of *A. maculatum* addition, with predator treatment and cover as fixed effects and tank as a random effect. Using SVL from 6 April or a calculated growth curve through both larval measurements and metamorph size did not alter these results.

Results

IG PREDATOR (*Ambystoma annulatum*)

Predator treatment significantly affected metamorph body condition of *A. annulatum*, but cover and the interaction of cover and predator treatment were not significant (Table 1). Post hoc tests showed metamorphs were smaller in body condition in the IGP-only and mosquitofish-only treatments compared to aeshnid-only, newt-only, aeshnid + newt and all predators (Fig. 2a). Larval period length was not affected by either predator or cover treatments, or their interaction (Table 1; Fig. 2b). Larval size of *A. annulatum* at the time of *A. maculatum* addition (ca. April 22) did not vary significantly by cover or predator treatments (Fig. A2 in Appendix S1).

We recovered 637 metamorphs and six larvae of *A. annulatum* at the end of the experiment. Survival of *A. annulatum* was significantly affected by predator treatment, but cover and their interaction were both not significant (Table 1). Survival was highest in the IGP-only and mosquitofish treatments (83% and 75%, respectively), both of which had significantly higher survival rates than all other treatments (Fig. 2c). The lowest average survival occurred with all three predators (17%), but post hoc tests showed this treatment was not significantly different from the aeshnids-only (42%) or aeshnids + newts (26%) treatments. Overall, 14% of metamorphs emerged with at least one injury. The prevalence of injuries on metamorphs was significantly influenced by predator treatment, but

cover and the predator–cover interaction terms were not significant ($\chi^2 = 35.98$, d.f. = 5, $P < 0.001$). IGP-only and newts-only treatments had the lowest number of injuries (Fig. 2d). The highest percentage of injuries were in the mosquitofish-only treatments (32% of individuals), and the overwhelming majority of injuries (93%) were of low severity, for example missing tail tips (Figs 2d and A3 in Appendix S1). The most severe injuries occurred more commonly in the tanks with aeshnids-only, aeshnids + newts and all three predators. In each case, 33–64% of the observed injuries included missing the entire tail, a limb or both (Fig. A3 in Appendix S1).

IG PREY (*Ambystoma maculatum*)

We saw no significant effects of predator treatment, cover treatment or their interaction on metamorph body condition, larval period length or survival for *A. maculatum* (Table 1; Fig. 2d–f). However, when we accounted for *A. annulatum* survival, we observed significant differences among treatments for all response variables (Tables A1–A3 in Appendix S1). Metamorph body condition of *A. maculatum* was significantly affected by a three-way interaction of top predator, cover and *A. annulatum* survival (Table 1). On average, metamorphs of *A. maculatum* had higher body condition when more *A. annulatum* survived (Fig. 3a–f). However, this pattern was reversed with mosquitofish-only; body condition of *A. maculatum* decreased when more *A. annulatum* survived in tanks without vertical cover (Fig. 3b; Table A1, Fig. A4 in Appendix S1). A similar negative pattern was observed with aeshnids + newts in the presence of cover, though the low overall variability in *A. annulatum* survival likely influenced this result (Fig. 3e).

The interaction of predator treatment with the survival of *A. annulatum* significantly affected the larval period length for *A. maculatum*, but no other higher order inter-

Covariate	Body condition	Larval period length	Survival
Ambystoma annulatum			
Predator	**11·44 (*P* = 0·04)**	1·79 (*P* = 0·88)	**17·81 (*P* = 0·003)**
Habitat	0·01 (*P* = 0·93)	0·12 (*P* = 0·89)	0·30 (*P* = 0·58)
Pred-Hab	4·78 (*P* = 0·44)	1·95 (*P* = 0·86)	1·67 (*P* = 0·89)
Ambystoma maculatum (without IG predator effects)			
Predator	4·93 (*P* = 0·42)	3·12 (*P* = 0·68)	6·49 (*P* = 0·26)
Habitat	1·30 (*P* = 0·25)	0·72 (*P* = 0·40)	0·01 (*P* = 0·94)
Pred-Hab	4·11 (*P* = 0·53)	1·16 (*P* = 0·95)	4·62 (*P* = 0·46)
Ambystoma maculatum (with IG predator effects)			
Predator	5·99 (*P* = 0·31)	21·27 (*P* = 0·001)	15·40 (*P* = 0·01)
Habitat	0·00 (*P* = 0·99)	0·37 (*P* = 0·54)	1·31 (*P* = 0·25)
AA	4·79 (*P* = 0·03)	7·75 (*P* = 0·005)	9·80 (*P* = 0·002)
Pred-Hab	11·17 (*P* = 0·05)	1·42 (*P* = 0·92)	14·91 (*P* = 0·01)
Pred-AA	9·87 (*P* = 0·08)	**14·73 (*P* = 0·01)**	10·31 (*P* = 0·07)
Hab-AA	0·25 (*P* = 0·62)	0·03 (*P* = 0·87)	0·98 (*P* = 0·32)
Pred-Hab-AA	**12·46 (*P* = 0·03)**	NA	**17·84 (*P* = 0·003)**

Table 1. Test statistics and *P*-values for body condition, larval period length and survival of ringed salamanders (*Ambystoma annulatum*) and spotted salamanders (*A. maculatum*) without and with accounting for the survival of *A. annulatum* survival. Values for body condition and larval period length are Wald's chi-square statistic and survival is likelihood ratio statistic, with *P*-values in parentheses. Pred = predator treatment, Hab = habitat treatment and AA = survival of *A. annulatum*. Degrees of freedom for each term are as follows: Predator = 5, Habitat = 1, Pred-Hab = 5, Pred: AA = 5, Hab-AA = 5, Hab: Pred:AA = 5
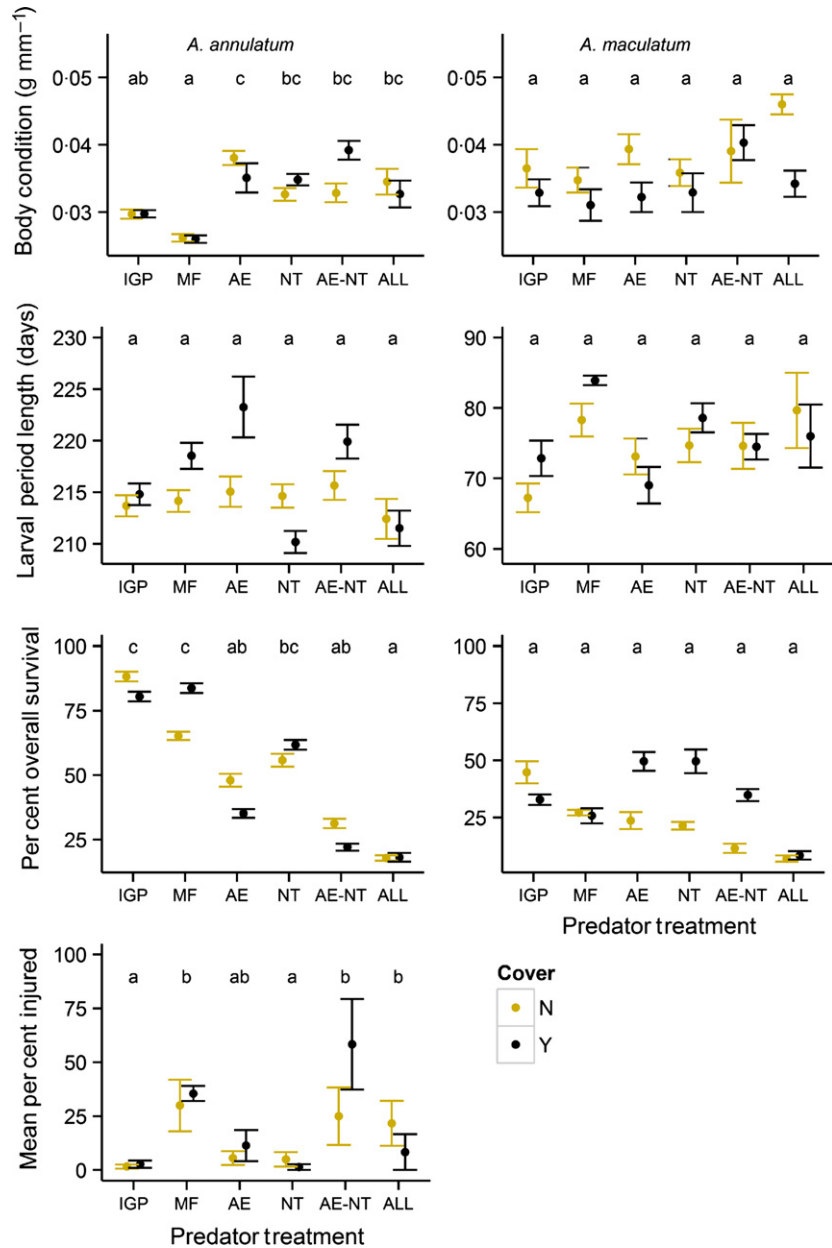
Bold values indicate statistically significant results ($P < 0.05$).

Fig. 2. Mean (±SE) body condition, larval period length and survival of ringed salamanders (*Ambystoma annulatum*; panels a–c) and spotted salamanders (*A. maculatum,* panels e–g) among the different predator and cover treatments. Panel d shows the mean (±SE) per cent of injured metamorphic ringed salamanders (*Ambystoma annulatum*) within predator food web and cover treatments. Gold circles/lines indicate the absence and black circles/solid lines indicate presence of habitat complexity. 'IGP' refers to no top predators present, 'MF' refers to mosquitofish only, 'AE' refers to aeshnids only, 'NT' refers to newts only, 'AE-NT' refers to aeshnid + newts, and 'ALL' refers to all three predators present. Sample sizes for the total number of metamorphs in each of the predator treatments (cover/no-cover) are as follows: IGP: 102/91; MF: 20/15, AE: 46/24, NT: 77/85, AE-NT: 60/67 and ALL: 34/22.

actions were significant (Table 1). Larval period length of *A. maculatum* had a positive relationship with *A. annulatum* survival in IGP-only treatment and in aeshnids-only treatments (Fig. 3g,i; Table A2, Fig. A5 in Appendix S1). This relationship switched to negative in tanks with all three predators (Fig. 3l) and showed no relationship with newts-only, mosquitofish-only or aeshnids + newts (Fig. 3h,j,k; Table A2, Fig. A5 in Appendix S1).

At the end of the experiment, we recovered 177 metamorphic and 92 larval *A. maculatum*. A three-way interaction of predators, cover and survival of *A. annulatum* significantly affected the number of metamorphs and overall survival of *A. maculatum* (Table 1). Overall survival showed a negative relationship with *A. annulatum* survival, but the slope of that relationship varied by predator and cover treatment (Fig. 3m–r). With aeshnids-

only, the absence of cover resulted in a switch to a positive relationship of *A. annulatum* and *A. maculatum* survival compared to a negative relationship in the presence of cover (Fig. 3o; Table A3, Fig. A6 in Appendix S1). A similar pattern existed with newts-only, where the covariance of survival among the two focal salamanders was only significant in the cover treatment (Fig. 3p; Table A3, Fig. A6 in Appendix S1). With all three predators, survival was extremely low for *A. maculatum* (<10%). The number of *A. maculatum* that remained larval was affected by predator treatment and *A. annulatum* survival, but no interaction terms were significant ($\chi^2 = 17.79$, d.f. = 1, $P < 0.001$). The per cent of individuals that remained larval was on average highest in tanks with mosquitofish-only (21%), newts-only (24%) and in the IGP-only treatment (14%).
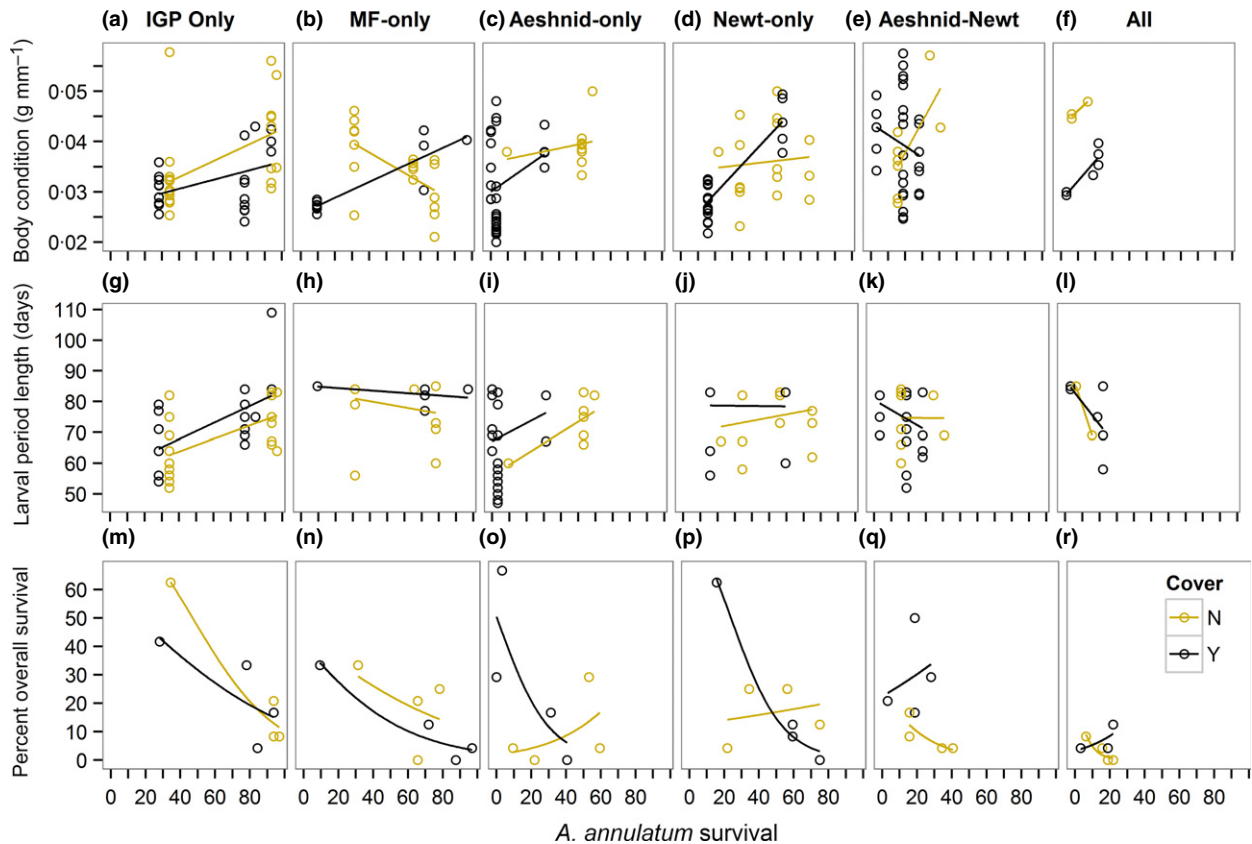
Fig. 3. Three-way interaction of predator treatment, habitat complexity and *Ambystoma annulatum* survival on metamorph body condition (a–f), larval period length (g–l) and survival (m–r) of *A. maculatum*. Bold names above each column of panels indicate the predator treatment. Gold circles/lines indicate the absence and black circles/solid lines indicate the presence of habitat complexity. Each dot is one individual salamander for body condition and larval period panels, and each dot is one tank in the survival panels.

Discussion

Both top predators and habitat complexity can affect IGP by influencing the IG predator, the IG prey or both. Furthermore, while synergistic effects of these two factors has been documented for some taxa (Finke & Denno 2006; Grabowski, Hughes & Kimbro 2008), their combined influence on IGP is largely untested and unknown for many taxa. Our study shows that (i) IG predators (*A. annulatum*) were affected by top predators but not habitat complexity, (ii) IGP was modified by the presence of top predators through their species-specific impact on the survival of the IG predator (*A. annulatum*) and (iii) habitat complexity altered IGP with some top predators but not others.

INFLUENCE OF TOP PREDATORS

Top predators often influence species interactions at lower trophic levels (e.g. Paine 1966; Dodson 1970; Morin 1983b), including IGP (e.g. McPeek 1998; Wissinger *et al.* 1999; Finke & Denno 2005). In particular, IGP is altered when top predators negatively impact the IG predator (Hall 2011). In our study, as the top predators reduced the survival of the IG predator, survival of the IG prey (*A. maculatum*) increased, typical of a density-mediated indirect effect (Abrams *et al.* 1996; Trussell, Ewanchuk & Matassa 2006). No top predators limited the growth of the IG predator such that they were too small to consume the IG prey, potentially because when mortality of the IG predator occurred, the survivors were released from intraspecific competition. Interestingly, larval size of *A. annulatum* was not different among treatments 6 weeks prior to metamorphosis, indicating that growth rates were homogenized despite variable survival – potential evidence for a behavioural shift. Wissinger *et al.* (1999) and Yurewicz (2004) both showed that IG predators experienced heightened mortality due to their higher activity rates compared with their IG prey. Predation also may not have occurred until late in the larval period of *A. annulatum*. Alternatively, density dependence may not have been strong enough to minimize predator–prey size disparities to the point where predation would be precluded (Rasmussen, Van Allen & Rudolf 2014). Body condition of the IG prey survivors increased in tanks with high predation rates, however, also likely due to reduced intraspecific competition. As size at metamorphosis in amphibians is strongly correlated with adult fitness (Semlitsch, Scott & Pechmann 1988; Scott 1994), this release from competition via predation could benefit IG prey.

While we did not observe a statistically significant increase in mortality with our additive design, the variance in survival for each salamander was much reduced with all three predators, indicating some additivity among predators, similar to other studies with multiple lethal predators (Relyea & Yurewicz 2002). Yet, not all predators had equivalent effects, supporting the hypothesis that different predator species can have dissimilar effects on prey populations and community structure (Relyea 2001; Chalcraft & Resetarits 2003). The presence of aeshnids resulted in high mortality regardless of predator combination, potentially from their sit-and-pursue hunting tactics and reduced gape limitations that often results high prey mortality (Preisser, Orrock & Schmitz 2007; Davenport, Hossack & Lowe 2014). This supports the idea of a sampling effect, where one predator contributes disproportionately to prey mortality compared with the other species are present (Ives, Cardinale & Snyder 2005). Our study also did not include all possible combinations of top predators, which we recognize limits our understanding of how multiple top predators influence IGP.

Mosquitofish are often a devastating invasive species that strongly affects aquatic food webs (Segev, Mangel & Blaustein 2009; Shulse & Semlitsch 2013). However, we saw nearly equivalent levels of survival in the IGP-only treatment compared with mosquitofish as top predators, indicating their deleterious effects on amphibian recruitment may be density-dependent. Body condition at metamorphosis for *A. annulatum* was the smallest in tanks with mosquitofish and metamorphs had substantially more injuries, despite equivalent survival to the IGP-only treatments, indicating indirect and/or sublethal costs to coexisting with mosquitofish. Interestingly, *A. maculatum* and *A. annulatum* metamorphosed at the same size from tanks with mosquitofish but at disparate survival rates (higher for *A. annulatum*). The highest proportion of individuals remaining as larvae for *A. maculatum* also occurred in the mosquitofish treatment, indicating that the predominant effects on *A. maculatum* were from *A. annulatum*, but that mosquitofish continued to affect *A. maculatum*'s ability to metamorphose.

In contrast to mosquitofish, aeshnids had the greatest negative impact on larval survival. Yet, we did not see the extreme mortality observed in other studies, which is surprising given our experimental duration was 10 months rather than days or weeks (e.g. Relyea & Yurewicz 2002; Yurewicz 2004; Hossie & Murray 2010). Predation by aeshnids may have been minimized due to our use of multiple dragonfly naiads, as other studies have shown that dragonfly predation rates saturate as their density increases due to behavioural interference (Ramos & Van Buskirk 2011). We observed some cannibalism among naiads despite using equivalently sized individuals, but the extent to which this occurred is somewhat unknown; thus, naiad density may confound our results and explain the large variance in response variables within dragonfly treatments.

Finally, newts had the weakest lethal and sublethal effects on both salamanders, which was not surprising given that they have the narrowest gape, resulting in a limited temporal period where consumption can occur before larvae grow into an invulnerable size class. Newts often forage on amphibian egg masses and can substantially reduce embryonic survival (Morin 1983a; Drake *et al.* 2014), and thus, our use of free-swimming hatchlings may have reduced their impact.

INFLUENCE OF HABITAT COMPLEXITY

Habitat complexity can have contrasting effects on predation rates. For some predators, cover reduces consumption by providing refuges from predators (e.g. Finke & Denno 2002; Warfe & Barmuta 2004), though substantial non-consumptive effects can subsequently occur (Orrock *et al.* 2013). Alternatively, cover has been shown to have minimal effects on some predators, primarily because of their hunting strategy or body size (e.g. Babbitt & Tanner 1998; Carey & Wahl 2010; Toscano & Griffen 2013). Our study supports this latter point, as cover did not have strong effects on metamorph traits, injury prevalence and survival for *A. annulatum*, and limited effects on *A. maculatum* that acted only in concert with specific predators. Although our cover matches cattails in form, one possible explanation for the reduced habitat effects is that it was still structurally simple; other studies have shown that structurally simple cover does not influence predators compared to more complex cover (Warfe & Barmuta 2004). All three predators and both salamanders were observed to use the vertical cover more often than the open side of the tank (mean ± SE number of larvae observed on open versus cover sides: 1.21 ± 0.04 vs. 1.93 ± 0.05, Thomas L. Anderson, unpublished data), but it may not have been dense enough to restrict predator foraging behaviour.

INTERACTION OF TOP PREDATORS AND HABITAT COMPLEXITY

We observed that certain predators in complex habitats had disproportionate effects on the IGP module, similar to Finke & Denno (2006) and Grabowski, Hughes & Kimbro (2008) who each found that different predator species had variable effects on interactions at lower trophic levels that depended upon habitat type. In our study, increased habitat complexity reversed the relationship of *A. annulatum* and *A. maculatum* survival (no effect to negative with newts or aeshnids). In the absence of cover, the positive relationship between *A. maculatum* and *A. annulatum* survival with aeshnids could suggest a behavioural response: *A. annulatum* may have foraged less on *A. maculatum* when there was no vertical cover to conceal the aeshnids, resulting in increased survival. The presence of cover for the mosquitofish treatment reversed the relationship of body condition of *A. maculatum* and *A. annu-*

latum survival from positive to negative, which could suggest that the few survivors did not benefit from thinning effects (e.g. Anderson & Semlitsch 2014) because zooplankton levels were potentially cropped back by mosquitofish. When cover was present, zooplankton may have had more refuge, though we did not collect quantitative data on this aspect of the food web. Further investigation of behavioural observations (Thomas L. Anderson, unpublished data) will potentially elucidate the mechanisms of such survival relationships among IG predator and prey with the different top predators in varying habitats.

IMPLICATIONS FOR NATURAL SYSTEMS

While predator food web complexity and IGP have strong experimental and theoretical underpinnings, observations from natural systems are needed to verify such findings for many taxa. For larval salamanders, experimental studies have shown larval IGP can be pervasive (Stenhouse 1985; Cortwright & Nelson 1990; Walls & Williams 2001; Anderson & Semlitsch 2014), yet inferences on long-term coexistence in natural populations in the light of such interactions have been infrequently investigated. Many ambystomatids co-occur in ponds with no direct evidence of exclusion either by predation or by competition (e.g. Ousterhout *et al.* 2015). We hypothesize that top-down predation may be a mechanism that permits coexistence. As permanent hydroperiod ponds typically contain high densities of top predators (Wellborn, Skelly & Werner 1996; Semlitsch *et al.* 2015), larval densities may be reduced such that their pairwise interactions are minimized, similar to our treatment with all three top predators, though *A. annulatum* still negatively affected recruitment of *A. maculatum* in some natural populations (Anderson *et al.* 2015). In ephemeral ponds, we hypothesize IGP would be amplified, as pond drying would reduce invertebrate predator density, leaving larval ambystomatids as top predators. Other prey species may provide alternative food sources that mediate both IGP and predation by top predators, though Davenport & Chalcraft (2012) found that alternative prey did not reduce top predators. Additional investigations of habitat complexity and predator food webs are needed for natural populations (e.g. Hartel *et al.* 2007), as documenting such context-dependent interactions are critical to elucidating the mechanisms that promote coexistence in natural populations, for both this and other systems (Agrawal *et al.* 2007).

CONCLUSIONS

Top predators and habitat complexity frequently alter the strength or outcome of pairwise species interactions. Yet, experiments that investigate such factors often simplify their various complexities in order to test for the influence of specific mechanisms. All but the simplest of communities have many organisms that co-occur and interact with one another, and thus, interactions among two links of a food web would be inextricably linked to what community members are also present, in addition to the habitat in which such interactions occur. Identifying these critical biotic or abiotic components will continue to help elucidate the mechanisms that determine the function and structure of food webs.

Data accessibility

All data are available in the Dryad Digital Repository http://doi.org/10.5061/dryad.66j20 (Anderson & Semlitsch 2015).

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Supporting Information

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

Appendix S1. Parameter estimates and additional figures for ringed salamanders (*Ambystoma annulatum*) and spotted salamanders (*A. maculatum*).