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Foraging under the risk of cannibalism leads to divergence in body size among tiger salamander larvae

Received: 5 October 1999 / Accepted: 8 February 2000

Abstract Populations of plants and animals are almost always made up of individuals of different sizes. In populations where cannibalism is common, this size variation can influence rates of mortality and growth and affect population regulation. Size variation can be caused by a variety of mechanisms. One of these is due to size-specific responses to the threat of predation by potentially cannibalistic conspecifics. We investigated the role of anti-predator behavior in size structure development within single-aged cohorts of Arizona tiger salamander larvae. In a laboratory experiment, we show that size variation increases over time within groups of salamanders, even if they are fed in isolation. We also show that increasing the size of neighbors decreases the feeding rate of small salamander larvae. However, increasing density of neighbors did not have a significant effect on feeding rate. These results are consistent with the hypothesis that size variation among tiger salamander larvae is, in part, a result of size-specific responses to predation risk. We discuss the potential for feedback between size structure development, predation risk, and rates of cannibalism.

Key words Cannibalism · Foraging · Predation · Risk · Size structure

Introduction

The importance of size structure in cannibalistic populations

Most populations of plants and animals include individuals of various body sizes. The pattern of size variation

can influence fecundity and mortality and can affect population regulation (Lomnicki 1988). Size structure, or the distribution of body sizes, can also influence individual fitness since body size is often related to feeding rate (Peters 1983), reproductive success (Peters 1983), social dominance (Abbott and Dill 1989), and predation risk (Fox 1975; Polis 1981). Some of these fitness effects are a direct result of body size while others depend on the relative position of an individual within a particular size distribution.

In many populations cannibalism can be an important source of mortality. In these cases the frequency distribution of body sizes can influence population growth. The rate of cannibalism is sensitive to size variation (Fox 1975; Polis 1981; Maret and Collins 1994) and even small amounts of cannibal activity can have large effects on density-dependent population regulation (Polis 1981). Therefore, in a population where cannibalism is common, factors that affect the development of size differences between individuals can influence population dynamics (Crowley and Hopper 1994). In this study, we investigated the interactions between the threat of cannibalism and the development of size differences among individuals. We tested the hypothesis that the development of size structure in a cannibalistic cohort of salamander larvae is, in part, due to individual variation in foraging behavior under the threat of cannibalism.

The mechanisms of size structure development

Size variation is often a result of differences in age. When conspecifics of different ages live together in the same habitat there can be strong, asymmetric competitive and predatory interactions among age classes (Persson 1988). Even in single-aged populations, however, size variation can develop along with similar asymmetric interactions (Uchmanksi 1985; Lomnicki 1988).

In a group of even-aged organisms, the emergence of size variation depends on differences among individuals in feeding rates or metabolic cost. To have consistent ef-

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fects on size structure development, these differences must also be related to body size. If larger individuals acquire resources faster than smaller individuals, they will also grow faster. If this difference exceeds the metabolic cost associated with larger size (Persson 1988), size variation will increase over time. Alternatively, if the difference in feeding rates between large and small individuals is less than the increased cost of larger size, size variation will decrease over time. This interplay between relative advantages of small and large body size determines the dynamics of size variation (Uchmanski 1985) and subsequent cannibalism (Dong and Polis 1992).

How do larger individuals gain a relative foraging advantage? In some cases foraging rate can increase with size faster than metabolic costs. This may be due to increased performance of the feeding apparatus (Peters 1983), or overcoming gape limitation and utilizing new food resources unavailable to smaller individuals (Nakamura and Kasahara 1956; Smith and Petranka 1987; Osenberg et al. 1992). Larger individuals may also actively suppress the feeding activity of smaller individuals (Crowley et al. 1987; Smith 1990). For example, large plants can shade smaller competitors (Weiner 1990), and large animals can defend territories with higher resources (Baird et al. 1996; Iguchi 1996), or steal food (Rivault and Cloarec 1990). In some populations, large individuals might consume smaller individuals, thereby gaining access to a rich food source obviously not available to smaller conspecifics (Fox 1975; Polis 1981).

Threat-sensitive foraging and size inequality

A more subtle advantage to large body size can develop in populations that experience high rates of cannibalism. Smaller conspecifics may reduce their feeding rate in the presence of larger individuals to reduce the risk of detection and possible cannibalism (Crowley and Hopper 1994). A growing body of theory, and empirical results, support the idea that individuals balance the benefits of energy intake with the risks of predation while foraging (Sih 1982; Gilliam and Fraser 1987; Werner 1992; Werner and Anholt 1993; Lima 1998). These studies suggest that in the presence of a predator, a threat-sensitive individual might forage less since foraging movements attract the attention of potential predators. If smaller individuals reduce feeding in the presence of larger individuals this could lead to greater variance in feeding rates, a positive relationship between size and feeding rate, and increased size variation. In this study we tested the hypothesis that threat-sensitive foraging contributes to the development of size variation in even-aged cohorts of Arizona tiger salamander larvae (*Ambystoma tigrinum nebulosum*).

The study system

Arizona tiger salamanders are found in high-altitude, temporary ponds throughout central and northeast Arizo-

na. Adults breed in the spring shortly after snow-melt and generally leave the ponds after breeding. In ponds that dry yearly, tiger salamander larvae are all approximately the same age. Densities of larvae can be high (maximum 98 m⁻²) and physical interactions among individuals are common (authors, personal observations). Size distributions early in the season generally exhibit low variance (mean range: 12.9–16.3 mm snout-vent length, SVL; SD range: 1.15–2.10 mm). Larvae grow quickly and size variance increases over time (measured as coefficient of variation, CV). The magnitude of increase in size variance differs among habitats and can lead to differences in cannibal frequency (Maret and Collins 1994). Causes of variation in size are not fully understood for this system. However, previous field studies have shown that density and alternative prey availability are related to patterns of size structure development in this species and other ambystomatids (Van Buskirk and Smith 1991; Loeb et al. 1994) and one laboratory study showed alternative prey availability caused an increase in size variation and cannibalism (Maret and Collins 1996).

In a previous study we showed that the difference in feeding rates between large and small larvae is greater in groups than in isolation (Ziembra and Collins 1999). This study also showed that the advantage to larger larvae, in groups, was due primarily to a reduction in feeding and growth rate among small larvae in the presence of larger individuals. The present study was designed to examine further the mechanism of feeding rate suppression in tiger salamander larvae.

In this study we ask why small salamander larvae reduce feeding activity in the presence of larger individuals. We propose three alternative hypotheses to explain reduced foraging activity among smaller larvae. We suggest that this behavior is due to: (1) a response to the risk of cannibalism by larger individuals, (2) the effects of direct physical interference, or (3) a size-dependent response to changes in the density of conspecifics. If small salamander larvae are responding to the threat of predation or injury by larger larvae (hypothesis 1), the reduced growth of small relative to larger individuals could exist even if larvae are isolated from one another during feeding. If the effect exists in the absence of feeding interactions this would rule out direct physical interference by the larger larvae (hypothesis 2). If hypothesis 1 were true, we would also predict that there would be a positive relationship between size differences within a group and the magnitude of the reduced foraging effect among smaller individuals. Since the threat of cannibalistic predation increases with increasing size variation between predators and prey (Fox 1975; Polis 1981; R.E. Ziembra, unpublished work), an individual larva would maximize fitness by responding to this size variation. A similar relationship should exist between density and feeding rate if hypothesis 3 is correct. We used two laboratory experiments to test these predictions of the risk-sensitive foraging hypothesis in Arizona tiger salamanders. In the first experiment we compared changes in size variation be-

tween groups of cohabiting larvae allowed to interact during feeding and groups not allowed to interact during feeding. The second experiment measured the effects of the size and density of neighbor salamanders on the feeding rate of a small focal individual. In this experiment we also manipulated food level to explore possible interaction with resource availability.

Methods

Does size-specific interference occur in the absence of feeding interactions?

Eggs were collected from 29-Mile Lake (34°28'22"N, 111°27'01"W) on 20 March 1997. All eggs were stored at room temperature until approximately 90% of the hatchlings had emerged. After hatching, larvae were kept in small 10-l plastic tubs and fed brine shrimp, *Artemia* sp., ad libitum. Within 1 week after hatching, a haphazard sample of 150 larvae was removed with a dip net and each larva measured (total length, mm) with a video imaging system (Optimas Inc.). Larvae were randomly assigned to one of three treatments.

The experiment consisted of three treatments designated isolated-fed isolated (I-I), grouped-fed isolated (G-I), and grouped-fed grouped (G-G). Each experimental unit consisted of a randomly selected group of ten salamanders. In the I-I treatment, larvae were held individually in 5-l-capacity plastic buckets containing 2 l of water. Each day all larvae in this group were moved to an identical set of buckets and fed 2 ml of a brine shrimp suspension containing the amount of brine shrimp hatching from 0.015 g of dry eggs. After 4 h of feeding, the larvae were moved back to the original buckets and the feeding buckets were cleaned. In the G-I treatment, all ten larvae were held in a single aquarium filled with 20 l of water with sides covered with white cardboard. Before feeding, these larvae were moved to individual buckets, where they were fed in isolation, then they were moved back to the aquarium. In the G-G treatment, larvae were always held in aquaria. For this treatment, we maintained two sets of aquaria, one for feeding and one for the rest of the day. We replicated all treatments five times.

After 2 weeks, all of the larvae were removed and total length (mm) was measured. Mean, CV, and the change in these variables over the period of the experiment were calculated for each group of ten larvae. All subsequent statistical comparisons were made using these groups. Since there were five groups in each treatment, $n=5$ for all tests. Differences between the I-I treatment and both the G-I and the G-G treatments were assessed using a sampled randomization test (Crowley 1992; Sokal and Rohlf 1995). In the randomization test, two sets of five coefficients of variation were sampled with replacement from the CVs calculated in the original 15 experimental units. The difference in the means of these two samples was used as a test statistic. Under a hypothesis of no difference between two treatments, this statistic has an expected value of zero. We calculated one-tailed P -values for the differences between treatment mean CV based on 5,000 replicate samples. This procedure was followed for each of three pairwise comparisons. An analogous procedure was used for analysis of growth rate (change in mean size). The randomization test was programmed in the S language using S-Plus statistical software (version 2000, Mathsoft Inc.).

Does density or size of neighbors affect the feeding behavior of small larvae?

Larvae for this experiment were laboratory-raised from a set of eggs collected from 29-Mile Lake on 20 March 1997. Each larva was placed in a small plastic cup, individually measured (total length in mm), and assigned to one of four contiguous size classes representing the entire range of the available size distribu-

tion (size classes I: 26–35 mm; II: 36–45 mm; III: 46–55 mm; IV: 56–65 mm total length). For each behavioral trial larvae were randomly selected from appropriate size classes.

All trials were performed in rectangular plastic containers holding 10 l of aged tap water. The experiment consisted of three treatments: density, food availability, and neighbor size variation. There were five levels of density: 0, 2, 4, 6, and 8 larvae from the smallest size class with one focal larva also from the smallest size class. For each level of the size variation treatment, three larvae from one of four size classes were held with one focal larva from the smallest size class. Two levels of food availability during the behavioral trials were fully crossed with both variation and density treatments. Low-food treatments received the amount of brine shrimp hatching from 0.06 g of dry eggs. High-food treatments received 3 times that amount.

Before each trial, larvae were placed in the plastic containers and allowed to acclimate for 5 h. During this time larvae interacted freely but no food was available. After the addition of food, we waited 5 min to allow the salamanders to begin feeding. Following this, behaviors of the focal larva were scored for 15 min. We measured the number of feeding attempts, tail movements, and physical interactions with other larvae. A feeding attempt was scored when the focal larva lunged and snapped at a prey item. We counted the number of tail movements or beats of the tail as an estimate of the amount of movement around the arena. Interactions were counted when any encounter between larvae resulted in a sudden escape response by the focal larva. If larvae touched each other but the focal larva did not swim away, we did not count this as an interaction.

Results from the density and size variation treatments were analyzed separately since they were not crossed in the design. To test for the effects of density or size variation and food level on feeding, movement, and interaction rates, we used a general linear model (S-Plus version 2000, Mathsoft Inc.). Both density and size variation were modeled as continuous variables and we assumed they were measured without error, while food level was modeled as a discontinuous fixed effect. Transformations did not improve the fit to a normal distribution for number of feeding attempts and movement rate and deviations from normality were not severe. A square-root transformation normalized the distribution of interactions and was used prior to statistical analysis.

Results

Does size-specific interference occur in the absence of feeding interactions?

Mean absolute growth rates ranged from 0.83 mm day⁻¹ to 0.85 mm day⁻¹ and did not differ among treatments (G-G vs. G-I, $P=0.988$; G-G vs. I-I, $P=0.854$; G-I vs. I-I, $P=0.812$; Fig. 1A). Change in coefficient of variation

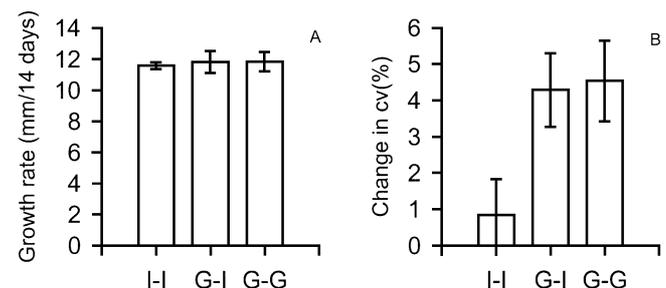


Fig. 1 Effect of grouping on mean growth rate over **A** 14 days and **B** change in CV%. Means and SEs are plotted for each treatment (I-I isolated/fed isolated, G-I grouped/fed isolated, G-G grouped/fed grouped)

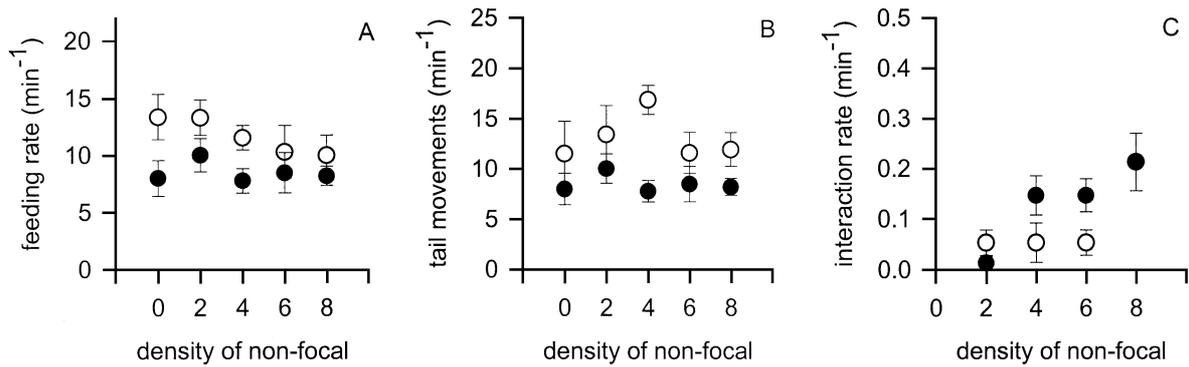


Fig. 2 Effect of density of same-sized neighbors on **A** rates of feeding, **B** movement, and **C** interactions with conspecifics. Means and SEs are plotted for each of five densities per tank. Two food levels are also plotted (low filled symbols, high open symbols). In **C** interactions were not defined for density=0 and therefore were not plotted

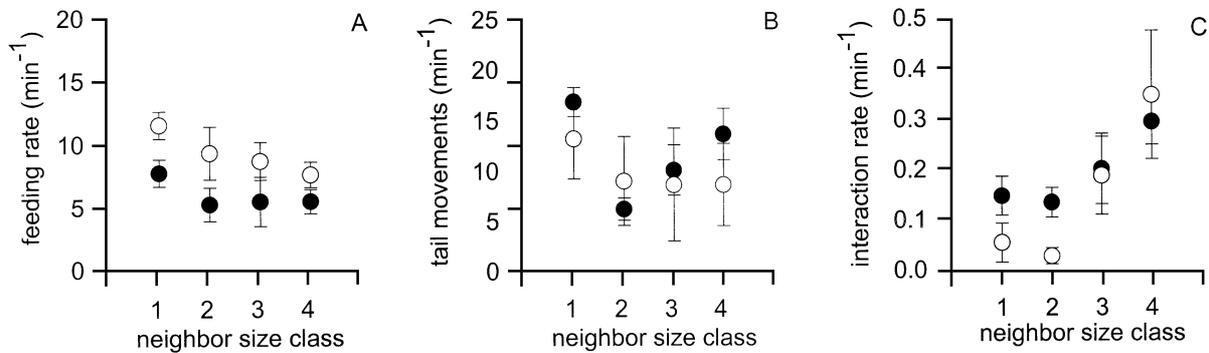


Fig. 3 Effect of size of neighbors on **A** rates of feeding, **B** movement, and **C** interactions with conspecifics. Means and SEs are plotted for each of four size classes of neighbors. Two food levels are also plotted (low filled symbols, high open symbols)

Table 1 Results from general linear model for the effects of density and food level on feeding rate, tail movements, and interaction rate

Source of variation	<i>df</i>	Sum of squares	<i>F</i>	<i>P</i>
Feeding rate				
Food level	1	129.28	11.27	0.0016
Density	1	29.59	2.58	0.1150
Food×Density	1	18.43	1.61	0.2112
Residual	46	527.57		
Tail movement				
Food level	1	0.115	0.01	0.9434
Density	1	7.40	0.33	0.5703
Food×Density	1	14.04	0.62	0.4350
Residual	46	1041.31		
Interaction rate				
Food level	1	0.05	2.40	0.1284
Density	1	1.03	45.11	<0.0000
Food×Density	1	0.04	1.62	0.2905
Residual	46	1.05		

was higher in the G-I treatment ($\Delta CV=4.29\%$), where larvae were raised in groups but fed in isolation, than in the I-I treatment ($\Delta CV=1.11\%$) (difference in mean $\Delta CV=3.18\%$, one-tailed $P=0.024$, Fig. 1B), where larvae were both raised and fed in isolation. Change in CV was higher in the G-G treatment ($\Delta CV=4.54\%$), where larvae were always in groups, relative to the I-I treatment (difference in mean $\Delta CV=3.43\%$, one-tailed $P=0.014$, Fig. 1B). There was no difference in change in size variation between G-G and G-I treatments (difference in $\Delta CV=0.25\%$, one-tailed $P=0.440$, Fig. 1B).

Does density or size of neighbors affect the feeding behavior of small larvae?

In the density experiment, there was no effect of density on feeding rate. Feeding rate was higher in the high-food treatments than in the low-food treatment, and there was not a significant interaction between density and food level. There were no main treatment or interaction effects on movement rate in the density experiment. Interaction rate increased with increasing density of non-focals, but there was no effect of food level or any inter-

action between food and density on interaction rate (Table 1, Fig. 2).

In the size variation experiment, feeding rate declined with increasing neighbor size. Feeding rate was also higher in the high-food treatment than in the low-food treatment. We did not detect a significant interaction effect between neighbor size and food level. As in the density experiment, movement rate was not affected by any

Table 2 Results from general linear model for the effects of neighbor size class and food level on feeding rate, tail movements, and interaction rate

Source of variation	<i>df</i>	Sum of squares	<i>F</i>	<i>P</i>
Feeding rate				
Food level	1	109.12	11.42	0.0018
Size class	1	46.02	4.81	0.0347
Food×Size	1	4.17	0.44	0.5132
Residual	36	344.07		
Tail movement				
Food level	1	33.61	1.23	0.2752
Size class	1	49.07	1.79	0.1890
Food×Size	1	8.93	0.33	0.5714
Residual	36	985.66		
Interaction rate				
Food level	1	0.18	5.66	0.0227
Size class	1	0.51	16.18	0.0002
Food×Size	1	0.10	3.11	0.0861
Residual	36	1.13		

treatment and no interactions were detected. Interaction rate was higher in the low-food treatment than in the high-food treatment and tended to increase with increasing size of neighbors, but we did not detect any interaction between treatments (Table 2, Fig. 3).

Discussion

The first experiment showed that change in size variation over time was higher in the G-I and G-G treatments relative to the I-I treatment. In other words, variation in growth rate among larvae raised in groups (G-I and G-G treatments) was greater than variation among individuals raised in isolation (I-I treatment), even if they were all fed in isolation (G-I treatment). We predicted that change in coefficient of variation would be higher in G-I than I-I if there were a size-specific interference effect in the absence of feeding interactions. Since change in CV was not significantly different between G-G and G-I treatments, we conclude that there were no additional size-specific interference effects when larvae were allowed to feed together. This implies exploitative competition for food was not a significant component of size-specific interactions in this experiment. The lack of any treatment effects on growth rate is consistent with this conclusion. However, this does not mean that size-independent or size-dependent exploitative competition would not occur if food were more limited. From these data we can conclude that some kind of size-specific interference among tiger salamander larvae can occur in the absence of exploitative effects.

The second experiment was designed to determine whether the size-specific interference effect seen in this and another study (Ziembra and Collins 1999) was due to a response to density or, alternatively, to a response to the presence of larger conspecifics. We saw no overall

effect of density on feeding rate. However, there was a significant decline in feeding rate with increasing neighbor size. Therefore, reduced foraging among smaller larvae is due to a response to size variation and not a result of responses to density. Inspection of the plots suggests some heterogeneity in slopes between food levels. However, we did not have enough statistical power to detect this effect (Tables 1, 2). Further studies will be necessary to elucidate this pattern.

We predicted that if the threat-sensitive foraging hypothesis explains size divergence in salamanders, reduced feeding rate among small larvae should be related to size variation, and therefore, relative risk. Our results support this hypothesis. However, we also found interaction rate increased with both increasing density and size variation. An alternative to the risk-sensitive foraging hypothesis may be that reductions in foraging rate are simply due to an increase in interaction rate – when individual larvae are involved in interactions they cannot feed. Several lines of evidence suggest that this is not a viable hypothesis to explain the size-specific interference effect. First, simple interference would occupy time for both interactants. Since the interference shown in this system is size-specific, small larvae would need to be affected more than larger larvae. If two individuals were involved in an interaction, time lost to interacting would be the same for both. Second, the results of the first experiment, although measuring only growth, showed that interference occurred in the absence of interactions during feeding. If that result is due in part to changes in feeding rate, this would indicate the hypothesis involving only interaction rate is not likely. Third, if interaction rate were solely responsible for the decrease in feeding rate, we would expect to find a relationship between interaction rate and feeding rate across all experimental units. We found low correlations between these two variables in both the density experiment ($r=-0.289$) and the size variation experiment ($r=-0.0335$). However, the correlation is higher for the density experiment and it is possible that physical interactions did have some direct effects on feeding rate in this experiment.

We have interpreted the size-specific interference effect in tiger salamanders as a consequence of threat-sensitive foraging strategies among individuals of different sizes. In a cohort of tiger salamander larvae, individuals of many different sizes coexist at the same time (Maret and Collins 1994). Since cannibalism in this species is common, each larva is under risk of predation by all individuals greater than approximately 100% larger (R.E. Ziembra, unpublished work). Furthermore, all larvae are actively growing and size relationships among individuals may change very rapidly. Therefore, the optimal feeding rate – one that maximizes future reproductive success – should be a complex function of a larva's position in the size distribution and potential for future growth (Crowley and Hopper 1994). This model predicts food level will have an effect on the magnitude of size-specific interference. When food is plentiful, reductions in feeding rate may be beneficial by balancing the costs

of foraging under predation risk. When food is scarcer a more moderate response to predators may occur since additional risks of starvation or extremely slow growth rate come into play. In temporary ponds, these costs could be particularly high (Wilbur 1984). Although we did not have enough data to test these predictions, in principle they should be relatively simple to test.

A key question arises from the application of the threat-sensitive foraging hypothesis to early divergence in size among larval tiger salamanders: Why do larvae respond to individuals that were initially similar in size (in the first experiment)? There are at least two possible explanations. It is not known how the sensory system involved in sensing conspecifics functions or how accurate it is. It is possible that an individual larva responds to conspecifics of similar size because information concerning actual size differences is unreliable. Another possibility is that interactions with conspecifics of similar sizes, while not often resulting in predation, may result in damage or injury. Such injuries have been documented in other salamanders and other amphibians (Van Buskirk and Smith 1991; Harris 1989).

The mechanism for size divergence we have proposed in this paper would have interesting consequences for population dynamics of tiger salamanders. We expect variation both within and between populations in sensitivity to the threat of cannibalism as food levels, cover availability, pond drying, and other factors vary. These factors affect the tradeoff in growth and mortality that determine optimal foraging behavior. Decreased sensitivity would have the effect of reducing overall size variation and, therefore, cannibalism rates. However, if size variation is increased by some other mechanism, for example, environmental heterogeneity (Voss 1993) or alternative prey availability (Nakamura and Kasahara 1956; Maret and Collins 1996), decreased sensitivity would increase capture rates of existing cannibals. Increased sensitivity would lead to higher variance in size, but lower capture rates for cannibals due to reduced ability to detect prey. The direct effects of cannibalism (mortality) can also have effects on size variation. It is not known how these conflicting effects would be resolved in natural populations.

Some behavioral interactions among tiger salamander larvae are based on the risk of conspecific predation. This behavioral response to conspecifics both results from the threat of cannibalism and affects future rates of cannibalism (Dong and Polis 1992). Understanding how foraging behavior evolves in the context of cannibalism will be critical to increasing our knowledge of linkages between behavior and population dynamics in natural systems.

Acknowledgements We would like to thank Peter Bednekoff, Chad Johnson, and one anonymous reviewer for helpful comments on a previous version of this manuscript. We would also like to thank Phil Crowley for advice on randomization tests. This work was supported by a grant from Sigma Xi (R.E.Z.) and NSF – Undergraduate Mentorships in Environmental Biology (M.T.M.).

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