

Potential of prey size and type to affect foraging asymmetries in tiger salamander (*Ambystoma tigrinum nebulosum*) larvae

Eric B. Johnson, Paulette Bierzychudek, and Howard H. Whiteman

Abstract: Although competitive interactions within predator populations are known to depend on their size structure, we understand less about how these interactions are influenced by prey characteristics. Most studies of such interactions for tiger salamander (*Ambystoma tigrinum nebulosum*) larvae have used small zooplankton prey. We investigate the potential of exploitation and interference competition to influence the success of tiger salamander larvae feeding on relatively large prey, mayfly and damselfly larvae. We measured salamander foraging efficiency for a range of salamander and prey sizes and observed aggression levels of salamanders of varying size housed together. Exploitative foraging efficiency (captures per attempts) increased with salamander size but was better predicted by relative prey size (prey size as a percentage of salamander snout-vent length) than by salamander size alone; it also depended significantly on prey type. Aggression (interference) levels were higher when prey were present, and larger salamanders were more aggressive than smaller ones but did not consume more mayfly prey. Our results suggest that investigating the environmental conditions, particularly the prey characteristics, that influence size-based competitive advantages will lead to a better understanding of predator population dynamics.

Résumé : Alors qu'il est connu que les interactions compétitives au sein des populations de prédateurs dépendent de la structure en taille de la population, on sait moins comment ces interactions sont affectées par les caractéristiques des proies. La plupart des études sur le sujet chez les larves de la salamandre tigrée (*Ambystoma tigrinum nebulosum*) ont utilisé comme proies du zooplancton de petite taille. Notre étude examine comment la compétition d'exploitation et la compétition d'interférence peuvent influencer le succès de larves de la salamandre tigrée qui se nourrissent de proies relativement grosses, des larves d'éphéméroptères et de zygoptères. Nous avons mesuré l'efficacité de la quête de nourriture chez des salamandres sur une gamme de tailles de salamandres et de proies et nous avons observé le niveau d'agression de salamandres de tailles différentes en cohabitation. L'efficacité de la quête par exploitation de la nourriture (captures par essai) augmente avec la taille de la salamandre, mais elle est mieux prédite par la taille relative de la proie (taille de la proie en pourcentage de la longueur du museau au cloaque de la salamandre) que par la seule taille de la salamandre; elle dépend aussi de façon significative du type de proie. Les niveaux d'agression (interférence) sont plus élevés en présence de proies; les grandes salamandres sont plus agressives que les petites, mais elles ne consomment pas davantage de larves d'éphéméroptères. Nos résultats indiquent qu'une recherche des conditions du milieu, et particulièrement des caractéristiques des proies, qui influencent les avantages compétitifs reliés à la taille mène à une meilleure compréhension de la dynamique des populations de prédateurs.

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Introduction

Werner and Gilliam (1984) drew the attention of ecologists to the importance of individual variation in size within animal populations. Up until then, most models of competitive interactions treated all individuals as essentially equal in their effect on one another. The number of models explicitly

recognizing size variation among individuals has since increased (e.g., Schoener 1986; Lomnicki 1988; Caswell 2001), and the impact of such variation on the outcome of intra- and interspecific interactions has been demonstrated (e.g., Brunkow and Collins 1996; De Roos and Persson 2001). However, size-structured models of predator population dynamics have typically explored only the consequences of

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variation in the body size of the predator population and not in the body size, or other characteristics, of their prey (De Roos and Persson 2001).

As both prey and predators grow, the size difference between them changes. Variation in the difference between body sizes of predator and prey can determine the nature of interactions between these individuals in several different ways: (i) prey can grow large enough relative to a predator that they reach a "size refuge" and are effectively no longer prey (Paine 1976; Olson 1996; Sommer et al. 1999), (ii) members of a species that competes with another species can grow large enough to prey on them instead of competing with them (Werner and Gilliam 1984; Polis et al. 1989; Wissinger 1992), and (iii) large individuals can escape from intraspecific competition by becoming cannibals, if they are large enough relative to other members of the population (Maret and Collins 1994; Claessen et al. 2000). More subtle effects of variation in size differences between predators and prey (i.e., changes in the strength of the interaction rather than in its direction) have been less well studied. To predict how such variation might affect predator-prey population dynamics, we need to know more about how and when variation in predator and prey sizes can affect the outcome of intraspecific competition among predators.

An individual's competitive ability can be understood as a combination of its metabolic requirements and foraging ability (De Roos and Persson 2001; Persson and Bronmark 2002). Because of the greater metabolic requirements of large body size, larger predators can be at a competitive disadvantage compared with smaller ones, unless there are size-based asymmetries in foraging success. When large animals have greater foraging success than smaller ones, this can compensate for their greater metabolic requirements and may provide larger animals with a competitive advantage (Persson 1985).

An individual's ability to exploit (capture) prey is one important aspect of foraging success. Exploitative ability often depends on a predator's body size. Furthermore, if the ability of animals to exploit prey depends on prey characteristics, such as size and species, as well as on predator size, then variation in the size structure and (or) composition of prey populations can affect the degree to which large body size confers a competitive advantage for predators.

Another mechanism that can give rise to size-specific differences in competitive ability is interference. To understand fully the relationship between size differences and competitive ability, the possible size dependence of interference behavior needs to be studied alongside that of exploitative behavior. Aggressive interactions are one form of direct interference. In general, the costs of aggression, such as the probability of injury or reductions in time spent foraging, are thought to decrease as the aggressor's size increases relative to that of its target (Case and Gilpin 1974; Polis 1988). If this is the case, the incidence of aggression by individuals should depend on their place in the size hierarchy, with larger animals being more aggressive than smaller ones. Aggressive acts can provide a competitive benefit to larger animals, either directly by providing a nutritional benefit or indirectly by imposing energetic costs on animals that are the targets of aggression. Although there does not appear to be a priori reasons for expecting prey size to directly impact

interference behavior, other resource characteristics that vary with prey size, such as the spatial distribution of prey, can influence the decision to defend a territory aggressively (Brown 1964; Grant 1993) and may also determine the net benefits of aggressive interference.

In this paper, we examine the size dependence of both exploitative and aggressive behavior in tiger salamander (*Ambystoma tigrinum nebulosum*) larvae. Size hierarchies have been well studied in larval tiger salamanders, perhaps because size differences between conspecifics can induce a cannibalistic morphology in large salamander larvae (Maret and Collins 1994). Furthermore, variation in prey attributes, namely the presence of relatively large macroinvertebrate or tadpole prey, has been shown to increase size variation among populations of tiger salamander larvae, leading to a greater frequency of cannibals (Loeb et al. 1994; Maret and Collins 1996; Whiteman et al. 2003). The mechanisms by which the presence of large prey increases size variation in their predators, however, are not understood.

Salamander larvae are gape-limited predators (Zaret 1980) whose food intake can decline as the size of the prey increases relative to salamander size (Smith and Petranksa 1987). To account for increased size variation in the presence of large prey, Maret and Collins (1996) proposed that foraging ability declines with relative prey size only when the prey is large relative to tiger salamander size, creating a competitive asymmetry between salamanders of different sizes when they are foraging on large prey but not on small ones. Exploitative size-based competitive asymmetries have not been found for large *Ambystoma opacum* larvae feeding on relatively small macrozooplankton prey (Smith 1990), but circumstantial evidence from stomach content analysis suggests that exploitative asymmetries do exist for small prey at earlier salamander developmental stages, when zooplankton are a relatively large prey for tiger salamanders (Dodson and Dodson 1971). Thus, there is reasonable evidence to suggest that relative prey size is an important determinant of foraging ability in *A. t. nebulosum*. However, the range of relative prey sizes for which this is so is not known. Furthermore, how any relationship between foraging ability and relative prey size might vary, depending on the prey species, is also unclear. Thus, the sizes and species of prey that give large salamanders an exploitative advantage are unknown.

It is unclear whether aggressive interference is an alternative mechanism that can explain the increase in size variation in the presence of large prey, although aggression is frequently observed in ambystomatid larvae (Semlitsch and Reichling 1989; Smith 1990; Walls and Roubesh 1991; Walls and Semlitsch 1991), and interference can reduce the growth rate of smaller salamander larvae relative to larger ones when they are housed together (Smith 1990; Van Buskirk and Smith 1991; Hokit et al. 1996; Ziemba and Collins 1999), even if the animals are isolated during feeding (Ziemba et al. 2000). Large salamander larvae have been found to be more aggressive than small ones (Brunkow and Collins 1998), and the presence of larger salamander larvae can also reduce the foraging rate of smaller ones (Ziemba et al. 2000).

However, all experimental studies of interference competition or aggressive behavior to date have used relatively small

prey (Smith 1990; Brunkow and Collins 1998; Ziemba and Collins 1999), whereas it is in the presence of larger prey that increases in size variation in tiger salamander populations have been observed (Loeb et al. 1994; Maret and Collins 1996; Whiteman et al. 2003). Thus, although aggressive interference can provide a relative benefit to larger salamanders when small prey are present, it is not clear if this is true in the presence of larger prey. Finally, it is not known whether aggression can provide a direct nutritional benefit to larger salamanders in addition to or instead of negatively affecting smaller salamanders.

To better determine the predator and prey sizes for which foraging ability increases with salamander body size, we ask these questions: (i) does variation in prey size and type (damselfly versus mayfly larvae) affect the prey capture efficiency of isolated tiger salamander larvae, (ii) is foraging efficiency independent of size when relative prey sizes are small but not when large and, if so, at what sizes, and (iii) when foraging on large prey, does aggressive interference provide large salamanders with a foraging advantage? To answer this last broad question, we ask four subsidiary questions: (1) are salamanders more aggressive when prey are present, (2) does a salamander make more aggressive acts as the size gap between it and other salamanders increases, (3) in the presence of a larger salamander, do small salamanders make fewer aggressive attempts, and (4) do larger salamanders garner more resources than smaller ones do?

Methods

Study site and organisms

Our study was conducted at the Rocky Mountain Biological Laboratory in Gothic, Colo., U.S.A. (2900 m above sea level). We seined tiger salamander larvae from a small temporary pond approximately 2 km south of Gothic. This pond is surrounded by grazed alpine meadow, has a silt and mud bottom, contains abundant emergent vegetation, and is less than 1 m deep.

Tiger salamander larvae are generalist foragers (Dodson and Dodson 1971; Leff and Bachman 1986) that add larger prey to their diet as they grow. Macroinvertebrates are among the largest prey consumed by noncannibalistic salamander larvae in ponds at Gothic (Dodson and Dodson 1971). We used two types of macroinvertebrate prey in this study: damselfly larvae (*Coenagrion resolutum* and *Enallagma cyathigerum*) and mayfly larvae (*Callibaetis* spp.). Both types co-occur naturally with tiger salamander populations in the field; however, damselfly larvae were often found in high densities in ponds containing salamander larvae, whereas mayfly larvae were only found in large numbers where salamanders were absent (personal observation). We collected damselfly and mayfly larvae from nearby sites.

We used clear plastic boxes (50 cm × 27 cm × 16 cm) containing 9 L of water as observation chambers for all experiments. Water was unchlorinated and was aged 24 h before use. The chambers were housed in a portable building that was heated to keep the water temperature of the chambers (which had a mean daily minimum of 17.4 ± 2.5 °C and a mean daily maximum of 25.6 ± 2.1 °C) similar to that of

outside ponds. Animals were cared for in accordance with the guidelines of the Canadian Council on Animal Care.

Foraging trials

We used efficiency of prey capture (number of captures per number of attempts) as a measure of foraging ability. All trials followed the same general procedure. First, we familiarized each individually housed salamander to a specific prey type in the following way. For each of 4 days, we fed each salamander one of the prey plus a supplement of 0.015 g of hatched brine shrimp (*Artemia* spp.) nauplii in case it could not catch the insect prey. After familiarization, salamanders were starved for 24 h and then placed individually into chambers. Salamanders were allowed to acclimatize to their chambers for 10–30 min. We then introduced 10 prey into the chamber. For the next 30 min, we recorded the number of successful and unsuccessful capture attempts. We defined an unsuccessful attempt as a lunge toward a prey item that did not result in its capture. Any prey eaten were replaced to maintain a constant prey density. At the end of the trial, we removed uneaten prey from the chamber, measured the snout–vent length (SVL) of the salamander, and measured water temperature. Chambers were cleaned with soap between trials, rinsed, and filled with new water. Each salamander was observed only once.

Although there was considerable size variation within both prey types, the damselflies that we used were generally larger than the mayflies. In all, we tested five different combinations of prey size and taxon based on the range of prey sizes available. We sorted the damselflies into three size classes, small (10–13 mm), medium-sized (14–17 mm), and large (18–21 mm), and divided the mayflies into two size classes, large (7–10 mm) and small (4–6 mm). Measurements were made from the front of the head to the base of the abdomen, not including cerci. The smallest salamanders tested could eat all size classes of prey but often took considerable time to swallow large damselflies. Most medium-sized and small damselflies and most mayflies were swallowed immediately. Some animals did not attempt to feed after capturing a prey item on their first attempt. We excluded such salamanders from the analysis because it is unlikely that their efficiency value of 1.0 accurately reflected their foraging ability.

We conducted trials at two different times to test the widest possible range of salamander sizes. At both times, we wished to represent the full extent of salamander size variation in the pond. To do so, we haphazardly selected equal numbers of salamanders from all size classes (in 2-mm SVL increments) after measuring all salamanders collected from the pond. We excluded any individuals expressing the cannibalistic phenotype.

The first damselfly trial, conducted 1–9 July 1997, used 21 salamander larvae: 6 (13–28 mm SVL) on small, 8 (15–29 mm SVL) on medium-sized, and 7 (17–27 mm SVL) on large damselflies. The second trial, conducted on 2 August 1997, when only large damselflies were available, used 13 salamanders (30–44 mm SVL).

We conducted the first mayfly trial concurrent with the first damselfly trial using 9 salamanders (19–31 mm SVL) on small mayfly larvae and 10 (19–33 mm SVL) on large

ones. During the familiarization period for these trials, 12 out of 19 salamanders developed gas bubbles in their stomachs and floated to the surface. Because this would have influenced their foraging ability, we replaced them with unfamiliarized salamanders.

An initial analysis of the results of this trial suggested that prey capture efficiency on large mayfly prey was independent of salamander size. To confirm these results, we conducted two supplemental trials with large mayfly prey. These trials used larger sample sizes to reduce the risk of making a type II error. One trial, conducted on 24 July 1997, used 23 animals (29–39 mm SVL) and the other, on 8 August 1997, used 36 animals (32–46 mm SVL). This second supplemental trial used animals that had been housed in the laboratory for 4 weeks as part of a separate growth experiment but that had never been tested for foraging efficiency. Because they had been fed primarily mayflies, we considered them already familiarized. These two trials were analyzed separately from the others.

To test whether variation in prey size and species can affect prey capture efficiency, we used multivariate linear regression models to determine if our ability to predict foraging efficiency was improved by including information about the size and type of the prey as well as salamander body size. We compared the variance explained by a model that included salamander SVL as a predictor of foraging efficiency with one that replaced salamander SVL with relative prey size (prey length as a percentage of salamander SVL). We calculated relative prey size conservatively using the lowest value of each prey size range.

Because the size of the mayfly larvae that we used did not overlap with those of the damselfly larvae, we could not analyze prey size and taxon as independent variables. However, we still wished to determine if foraging efficiency differed between different classes of prey, independent of any variation explained by salamander SVL or relative prey size. To do this, we created a new variable, “prey category”, having five levels: large and small mayflies and large, medium-sized, and small damselflies. Multivariate linear regression is most often conducted using continuous variables, but categorical data can be incorporated by creating a set of $N - 1$ dummy variables to represent the N categories of a variable (Neter et al. 1996). This approach allowed us to determine whether and how the effect of each level of prey category differed from the effect of the excluded level. Because large mayflies were the largest prey for which foraging efficiency was found to be size independent, we excluded this level of prey category from the model. (Excluding another level would not have altered the statistical results but would have changed their interpretation.) A significant regression coefficient for any of the dummy variables indicated that the mean foraging efficiency for that level of prey category differed from the mean foraging efficiency for large mayflies when the other predictors (in this case salamander SVL or relative prey size) were accounted for.

Water temperature was also tested as a predictor because it can influence the probability of capture in aquatic populations (Anderson et al. 2001). In the analysis, prey capture efficiency values were square root transformed to reduce heteroscedasticity and to account for nonlinearity.

Observations of aggression

We manipulated the competitive environments faced by salamanders by varying the size of a focal salamander relative to that of nonfocal salamanders housed in the same chamber. For these observations, we housed six salamanders in each chamber. Five of them, designated the nonfocal salamanders, were the same size in all treatments, 28–29 mm SVL. We chose the sixth, designated the focal salamander, to be either the same size as the nonfocal animals (1.0 \times treatment), 15% larger (1.15 \times), or 25% larger (1.25 \times). We clipped a notch in the tails of all focal salamanders to distinguish them from the nonfocal salamanders in the 1.0 \times treatment. Salamanders were fed daily using the feeding regime described below. Chambers were stacked in blocks of three, each block containing one chamber from each size treatment. This design was replicated six times for a total of 18 chambers. Each day, we rotated the vertical positions of the chambers within blocks as well as the respective horizontal positions of the blocks.

We conducted observations on 25–27 July 1997 after the salamanders had been housed in the above conditions for 2 weeks. Because one nonfocal salamander died, one chamber contained only four nonfocal salamanders during the observations. We included this chamber in our analysis but reduced feeding in it so that per capita food levels were consistent across chambers. Feeding levels consisted of one mayfly larva per salamander plus a supplement of 0.0075 g of brine shrimp nauplii per salamander to ensure that salamanders unable to capture mayfly larvae would survive the experiment. We observed the aggressive behavior of both focal and nonfocal salamanders for 10 min before feeding (1300–1530) and for 10 min during feeding (1600–1730 on the same day). We allowed the mayfly larvae to acclimatize by floating them in bowls in the chamber for 1–2 min prior to observations made during feeding. To begin the observation period, we allowed the mayfly larvae to swim from the bowl into the chamber and added the brine shrimp at the same time. Prey were not replaced during the trials; all mayflies were consumed by the end of each 10-min period.

We recorded two kinds of aggressive behaviors: lunges and bites. Walls and Jaeger (1987) defined these categories of overt aggression as “*Lunge*, one salamander rapidly and abruptly moves toward another individual, but does not intersect any part of that individual’s body... *Bite*, one salamander, with mouth open, grabs another.” Similar motions occur during unsuccessful and successful predation attempts, including cannibalism. Although it is possible that what we describe as “aggression” is closely linked to predatory behavior, our interest is simply in how this behavioral response, whatever the intent, varies by animal size and in its effect on the foraging success of individuals. For simplicity’s sake, we will refer to this behavior as aggression.

We also recorded the number of mayfly larvae eaten by focal and nonfocal salamanders. We did not observe patterns of brine shrimp consumption because the brine shrimp nauplii were too small and numerous to observe reliably.

We used a three-way MANOVA, with focal salamander size (1.0 \times , 1.15 \times , and 1.25 \times treatments), observation time (before versus during feeding), and block as main effects, to compare the frequencies of lunges. Because biting occurred

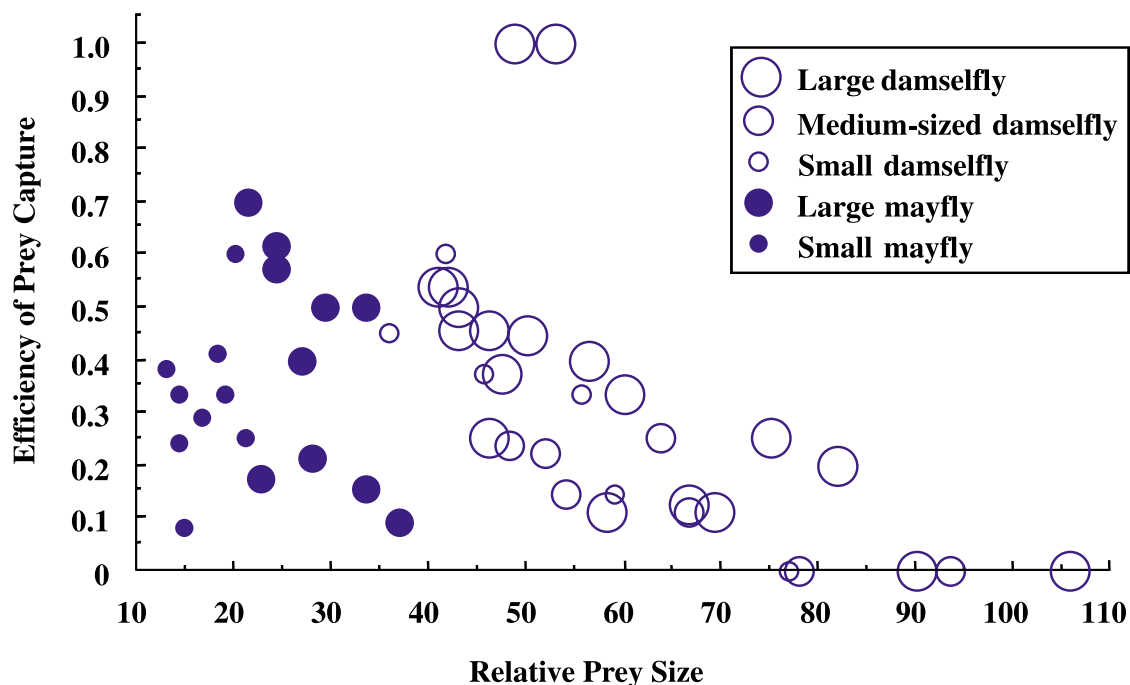
Table 1. Summary of regression model results for tiger salamander (*Ambystoma tigrinum nebulosum*) larvae foraging trials.

Source of variation	Model ^a		
	1	2	3
Constant	-0.056 (0.11)	0.95*** (0.061)	0.88 (0.58)
Salamander SVL	0.025*** (0.004)		
Relative prey size		-0.012*** (0.001)	-0.012*** (0.002)
Large damselfly	-0.23** (0.071)	0.34*** (0.074)	0.32*** (0.088)
Medium-sized damselfly	-0.21* (0.086)	0.17 (0.090)	0.15 (0.10)
Small damselfly	0.041 (0.092)	0.21* (0.084)	0.18 (0.095)
Small mayfly	-0.0093 (0.080)	-0.18* (0.070)	-0.20** (0.078)
Temperature			0.0012 (0.009)
<i>F</i>	11.70	19.18	15.34
Error sum of squares	1.37	1.01	0.99
Adjusted <i>R</i> ²	0.51	0.64	0.64

Note: Values presented are unstandardized regression coefficients with their standard errors in parentheses. *, $0.01 < p \leq 0.05$; **, $0.001 < p \leq 0.01$; ***, $p \leq 0.001$.

^aModel 1: SVL (snout-vent length) and dummy variables; model 2: relative prey size and dummy variables; model 3: relative prey size, dummy variables, and temperature.

Fig. 1. Efficiency of prey capture (no. of captures per attempts) as a function of relative prey size (prey length as a percentage of tiger salamander (*Ambystoma tigrinum nebulosum*) larvae snout-vent length) by prey category. Relative prey size ranges for each category of prey are as follows: large damselflies, 41%–106%; medium-sized damselflies, 48%–93%; small damselflies, 36%–77%; large mayflies, 21%–37%; small mayflies, 13%–21%.



with low frequency, it was not included in the MANOVA. We used two categories of lunges as dependent variables: those made by the focal animal and those made by nonfocal animals. In both cases, the number of lunges was square root transformed to reduce heteroscedasticity. We followed significant MANOVA results by ANOVA tests to clarify the contribution of each dependent variable. We used a two-way ANOVA, with salamander size and block as main effects, to analyze differences in focal animal mayfly consumption among size treatments. Because the feeding regime for a

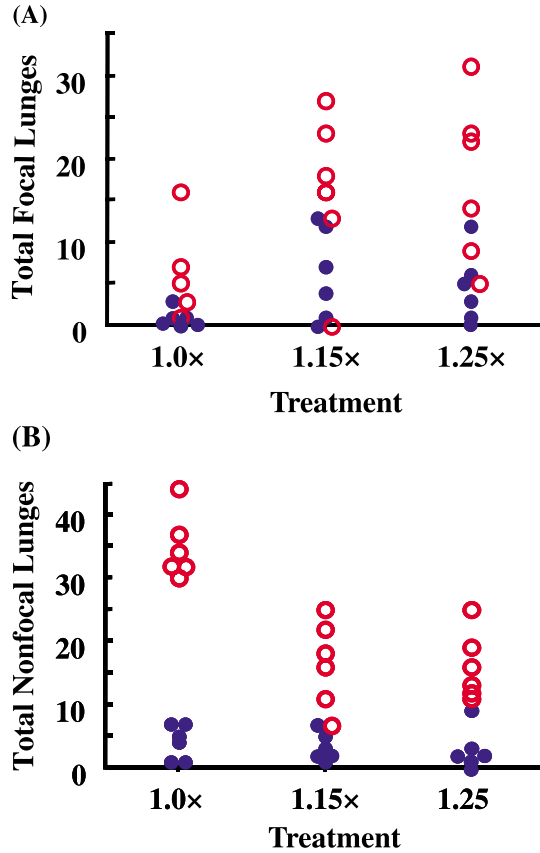
chamber consisted of one mayfly per salamander, focal consumption values greater than 1 indicate greater consumption of mayfly larvae by the focal salamander. All tests were performed using SPSS version 10.0 (SPSS Inc. 2000).

Results

Foraging trials

Foraging efficiency increased with salamander SVL (Table 1, model 1) and decreased as relative prey size increased

Fig. 2. Mean number of lunges made before (solid circles) and during (open circles) feeding by focal animal size treatment. (A) Lunges made by focal animals. (B) Lunges made by nonfocal animals. Treatment levels indicate the size of the focal salamander relative to that of nonfocal salamanders. *N* equals 6 for each treatment × time combination.



(Table 1, model 2; Fig. 1). Although salamander SVL and relative prey size were both significant predictors of foraging efficiency (Table 1), a regression model using relative prey size explained more variance than a model using SVL (adjusted $R^2 = 0.64$ versus 0.51). Thus, for the rest of the analysis, we use relative prey size as a predictor.

Removing the dummy variables representing prey category levels from model 2 resulted in a dramatic drop in the R^2 value of the model ($\Delta R^2 = -0.29$, $F^* = 10.21$, $p < 0.001$), indicating that the prey category levels contributed significantly to the variance explained by the model. Dummy variables representing prey category levels were significant predictors of foraging efficiency (Table 1, model 2). The significance of the regression coefficients for these variables indicates that mean salamander foraging efficiency depended on the prey category level, even when the effects of relative prey size were accounted for. Differences in mean foraging efficiency among prey category levels were complex. If the prey category levels are grouped based on the signs of their regression coefficients and the significance of their difference from the reference category (i.e., large mayflies), the ordering is “foraging efficiency on large and small damselflies” > “efficiency on medium-sized damselflies and large mayflies” > “efficiency on small mayflies”.

Table 2. Summary of MANOVA results for observations of aggressive behavior.

Source	Wilks' λ	<i>F</i>	Numerator/ denominator df	<i>p</i>
Size	0.086	10.85	4/18	<0.001
Time of observation	0.035	122.31	2/9	<0.001
Block	0.223	2.01	10/18	0.095
Size × time	0.274	4.10	4/18	0.016
Size × block	0.106	1.86	20/28	0.096
Block × time	0.273	1.64	10/18	0.17

Note: Values in boldface type are significant ($p \leq 0.05$).

Even though we saw size dependence in the main trials, where relative prey size ranged from 13% to 106% of salamander size, neither of the supplemental trials using large mayfly larvae showed a significant relationship between relative prey size and foraging efficiency ($F_{[1,33]} = 0.48$, $p = 0.49$, $R^2 = 0.14$; $F_{[1,20]} = 2.53$, $p = 0.12$, $R^2 = 0.11$). The range of relative prey sizes in these trials (15%–24%) overlapped with the lower end of the size range of the main trials.

Salamander foraging efficiency was positively correlated with water temperature (Pearson's correlation, $r = 0.56$, $p \leq 0.001$, $N = 52$). However, water temperature was also correlated with SVL (Pearson's correlation, $r = 0.42$, $p = 0.002$, $N = 50$) because the August trials, which tested the largest salamanders, had the warmest water temperatures. Including temperature in the model did not improve the fit of the regression model (adjusted $R^2 = 0.64$) (Table 1), neither was temperature a significant predictor of foraging efficiency ($t = 0.14$, $p = 0.89$).

Observations of aggression

Both focal and nonfocal salamanders were far more aggressive during feeding than before feeding (Fig. 2). Biting occurred less frequently than lunging; we observed up to 65 lunges during an observation period but never more than four bites. Biting did increase during feeding, however. Only one bite, made by a nonfocal animal, was observed before feeding, whereas during feeding, 14 bites were made by focal animals and 19 by nonfocal animals. Because biting was so infrequent, we were unable to test for differences between size groups and we focus on lunges for the rest of the analysis.

During feeding, the number of lunges increased from their prefeeding levels by three to nine times (Fig. 2). MANOVA results show that both the presence of prey and focal salamander size had a significant effect on the number of lunges (Table 2). Univariate tests indicate that the increase in lunges during feeding was highly significant, regardless of which animal initiated the lunge (Table 3, Fig. 2).

The effect of focal salamander size on the frequency of lunges differed for focal animals and nonfocal animals (Table 3). For focal salamanders, larger individuals were more likely to be aggressive. Focal animals in the 1.15x and 1.25x treatments made about three times the number of lunges as focal animals in the 1.0x treatment did (Fig. 2A) (Scheffé's post-hoc test, $p = 0.002$ and 0.006, respectively). The number of lunges did not differ significantly between focal ani-

Table 3. Summary of ANOVA results for observations of aggressive behavior and mayfly consumption.

Source	df	Mean squares	F	p
Lunges made by focal animals				
Size	2	12.98	14.78	0.001
Time of observation	1	32.41	36.90	<0.001
Block	5	2.89	3.30	0.051
Size × time	2	0.77	0.87	0.45
Size × block	10	1.28	1.46	0.28
Time × block	5	0.58	0.66	0.66
Error	10	0.88		
Lunges made by nonfocal animals				
Size	2	5.18	18.39	<0.001
Time of observation	1	76.41	271.23	<0.001
Block	5	0.33	1.17	0.39
Size × time	2	2.57	9.10	0.006
Size × block	10	0.71	2.52	0.081
Time × block	5	0.93	3.30	0.051
Error	10	0.28		
Mayfly consumption				
Size	2	1.56	1.90	0.20
Block	5	0.36	0.43	0.82
Error	10	0.82		

Note: Values in boldface type are significant ($p \leq 0.05$).

mals in the 1.15× and 1.25× size treatments ($p = 0.74$). Large focal animals appeared to suppress aggression among nonfocal animals. During feeding, nonfocal animals in the 1.15× and 1.25× treatments made fewer than half as many lunges as nonfocal animals in the 1.0× treatment (Fig. 2B). Again, these differences were significant (Scheffé's post-hoc test, $p \leq 0.002$ and 0.001 , respectively), whereas there was no significant difference between the 1.15× and 1.25× size treatments ($p = 0.74$). For lunges made by nonfocal animals, these size effects were important only during feeding, resulting in a significant interaction between the effect of size and the presence of prey (Table 3).

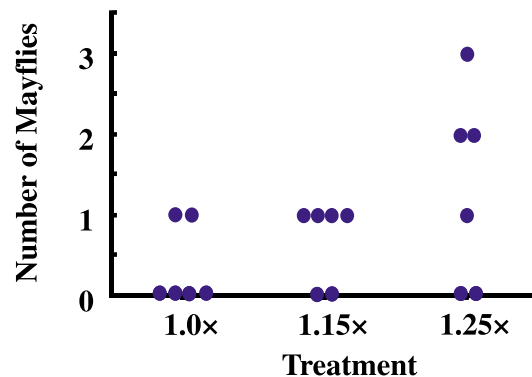
Although larger focal salamanders made more lunges than smaller focal salamanders, we did not find evidence that they consumed more mayflies during the trials. Some focal animals in the 1.25× treatment did catch more than one mayfly, whereas no focal salamander in the 1.0× or 1.15× treatment caught more than one (Fig. 3). However, this trend was not significant (Table 3).

Discussion

We observed size dependence of both exploitative and aggressive (interference) behavior in tiger salamander larvae. For neither type of behavior was this dependency straightforward. We will discuss the results of these two aspects of our study separately.

Foraging trials

Foraging efficiency increased as relative prey size decreased; salamanders that were larger with respect to their prey captured more prey per attempt than did smaller ones. Relative prey size (prey size as a percentage of salamander size) was a better predictor of foraging efficiency than was

Fig. 3. Number of mayflies consumed by focal salamanders. Treatment levels indicate the size of the focal salamander relative to that of nonfocal salamanders. N equals 6 trials for each size treatment.

salamander size alone; prey category also explained a significant amount of the variance in foraging efficiency. Thus, the degree to which large size was advantageous depended on the size and on the type of prey available.

In the supplemental trials, where prey never exceeded 24% of salamander size, we did not observe an increase in foraging efficiency with salamander size. Only in the main set of trials, in which prey ranged from 13% to 106% of body size, was a size advantage evident. This finding provides support for Maret and Collins' (1996) hypothesis that larger tiger salamanders can better exploit relatively large prey than small salamanders can but that there is no advantage to large size when prey are small. If our results translate into greater growth rates for larger individuals, we would expect that, over time, and only when salamanders are feeding on large prey, the size variation of a population of larval salamanders would increase. By contrast, for tiger salamanders feeding primarily on zooplankton, a common prey in these ponds (Dodson and Dodson 1971), we would not expect exploitative differences in foraging ability to increase size variation. Zooplankton seldom exceed 3 mm in length, and salamanders are approximately 10 mm long when they hatch, so zooplankton are at most 30% of salamander SVL at hatching, and their relative size decreases as the salamanders grow. Size dependence of foraging efficiency on zooplankton might be important in establishing initial size hierarchies, which may have consequences later in development, but its ability to increase size variation directly diminishes after that.

Because salamanders are known to be gape-limited predators (Zaret 1980), it is perhaps not surprising that larger individuals would be more successful. However, in our study, none of the prey exceeded the gape size of any of the salamanders. Apparently, foraging success can depend on relative prey size even when prey do not approach a gape-limiting size. We are uncertain what other mechanism might underlie the size advantage that we observed, but it is worth noting that in gape-limited fish, the depth (breadth) of prey can be a better determinant of maximum prey size than prey length (Hambricht 1991; Nilsson and Bronmark 2000).

We also found that foraging efficiency depended on the category of prey; even with relative prey size accounted for, foraging efficiencies still differed significantly among prey

category levels. There are at least three possible explanations for this result: (1) the relationship between foraging efficiency and relative prey size may be the same across prey taxa, but the functional relationship may not be as simple as was assumed by our statistical model, (2) the relationship may differ by prey taxon, but only in its intercept, and (3) the form (slope or shape) of the relationship may differ by prey taxon. Although the lack of overlap among the relative size ranges of the two prey taxa that we used prevents us from establishing with certainty which of these explanations is correct, a close examination of our results allows us to narrow the possibilities.

The average foraging efficiencies for the damselfly size categories were neither always higher nor always lower than those for the mayfly size categories. For this reason, the second explanation is unlikely. Another clue is that foraging efficiency did not depend on relative prey size in the supplemental trials, whereas it did in the main trials. The prey sizes used in the supplemental trials were among the smallest relative prey sizes tested. Thus, the functional relationship between relative prey size and foraging efficiency appears to have differed over the range of relative prey sizes that we tested. Once again, this makes the second explanation unlikely. Finally, a number of studies have revealed a hump-shaped relationship between foraging ability and predator body size, where foraging ability is thought to be low for small predators owing to their difficulty in capturing and handling prey but also low for large predators because of difficulties in detecting prey (see references in De Roos and Persson 2001). Although a hump shape is not clearly apparent from a graphical examination of our data, the foraging efficiencies for the prey category with the smallest relative prey size, small mayflies, are lower than those for the reference level, large mayflies, a finding consistent with this pattern. Future studies of foraging ability in salamander larvae should use sample sizes and relative prey size ranges large enough to specify accurately the functional relationship of size and foraging efficiency for different species to differentiate between the reasons listed above.

Observations of aggression

Mayfly consumption rates were not significantly higher for large focal salamanders than for smaller ones, an observation at odds with the hypothesis that large individuals have a foraging advantage during interference competition. However, our other results were consistent with that hypothesis. First, larger focal animals were more aggressive, i.e., they lunged more frequently than did focal animals that were similar in size to nonfocals. Second, larger focal animals suppressed lunging among nonfocal animals during feeding to a significantly greater degree than smaller focal animals did. Finally, the dramatic increase in aggressive behavior during feeding suggests that food resources acted as a cue for aggressive behavior.

It is puzzling that we should observe these differences in aggressive behavior between large and small individuals without observing a concomitant higher mayfly consumption rate. After all, there are costs to aggression, such as the probability of injury or reductions in time spent foraging. There are several possible explanations for our results, including two aspects of our study's design. (1) We placed

only one mayfly per salamander in the chambers and did not replace those eaten. With greater prey numbers, there would have been greater opportunity for larger animals to consume more prey. (2) Larger salamanders may have consumed more of the brine shrimp that we provided, but these were too small for us to measure their consumption rate. Beyond these considerations, if smaller salamanders were more likely to have been injured during the interaction, then despite similar consumption rates, they might manifest lower growth rates than larger salamanders, a growth pattern observed for salamanders interfering for small prey (Smith 1990; Ziemba and Collins 1999). Finally, it is important to consider the constraints imposed by our artificial environment as well. Although similar in many respects to the conditions under which most salamander behavior has been studied, our chambers were small, had no structural complexity, and contained only small numbers of mayfly prey. Under these conditions, salamanders may have continued to display the aggression that they typically do in nature but have been unable to reap its usual rewards.

There have been many other studies of interference behavior and its role in the population dynamics of larval salamanders (Smith 1990; Brunkow and Collins 1998; Ziemba and Collins 1999; Ziemba et al. 2000). But each of them has been conducted under somewhat different conditions (salamander sizes and prey presence-absence have varied among studies; relatively small prey are typically used), making it hard to generalize from them. Clearly, interference behavior and its effects differ based on characteristics of the predators (such as their sizes) and the experimental conditions; rigorously examining the consequences of variation in these conditions could do much to clarify the seemingly contradictory results of different studies. Furthermore, if the results of interference competition depend on resource conditions, then experiments using only one prey type may be unable to elucidate the conditions under which interference competition can increase size variation, and more studies may be needed to explore variation in this condition as well.

The foraging ability of an animal is a combination of both its exploitative and its interference abilities. Depending on the sizes of predators and prey present in a pond at any given time, both exploitative and interference mechanisms have the potential to give larger salamanders a competitive advantage. Smith (1990) has shown that for relatively small prey, interference, but not exploitative foraging ability, can give larger salamanders a competitive advantage. We show that for larger prey, larger salamanders have an exploitative foraging advantage and, if their greater aggression allows greater growth rates, will have an additional interference advantage as well. However, the relative contributions of exploitation and interference towards any overall foraging advantage enjoyed by larger animals still need to be determined. Furthermore, the degree to which these foraging advantages will increase size variation in a population will depend on how metabolic costs scale with body size.

Salamanders face a resource environment that is size structured and temporally variable. Studies of interspecific competition frequently relate competitive outcomes like coexistence, exclusion, and invasion to differences in how species exploit and directly interact (interfere) over resources (Tilman 1985; Goldberg 1996; Walls 1996; Faragher and

Jaeger 1998; Holway 1999; Kiesecker et al. 2001). Our results emphasize the important role that variation in prey size structure and composition may play in determining size-specific foraging abilities, and thus intraspecific competitive asymmetries, in larval salamanders. Furthermore, given the sensitivity of the aggressive defense of a territory to resource conditions (Brown 1964; Grant 1993), it seems plausible that changes in aggressive interference may also be related to resource conditions. For these reasons, focusing on individual variation in the specific mechanisms of resource use might prove as helpful in understanding intraspecific competitive outcomes as it has for interspecific competitive outcomes.

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