

Erica L. Wildy · Douglas P. Chivers
Joseph M. Kiesecker · Andrew R. Blaustein

The effects of food level and conspecific density on biting and cannibalism in larval long-toed salamanders, *Ambystoma macrodactylum*

Received: 4 October 2000 / Accepted: 27 December 2000 / Published online: 23 March 2001
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Abstract Previous studies have examined abiotic and biotic factors that facilitate agonistic behavior. For larval amphibians, food availability and conspecific density have been suggested as important factors influencing intraspecific aggression and cannibalism. In this study, we examined the separate and combined effects of food availability and density on the agonistic behavior and life history of larval long-toed salamanders, *Ambystoma macrodactylum*. We designed a 2×2 factorial experiment in which larvae were raised with either a high or low density of conspecifics and fed either a high or low level of food. For each treatment, we quantified the amount of group size variation, biting, and cannibalism occurring. Additionally, we examined survival to, time to and size at metamorphosis for all larvae. Results indicated that differences in both density and food level influenced all three life history traits measured. Moreover, differences in food level at which larvae were reared resulted in higher within-group size variation and heightened intraspecific biting while both density and food level contributed to increased cannibalism. We suggest that increased hunger levels and an uneven size structure promoted biting among larvae in the low food treatments. Moreover, these factors combined with a higher encounter rate with conspecifics in the high density treatments may have prompted larger individuals to seek

an alternative food source in the form of smaller conspecifics.

Keywords Cannibalism · Aggression · Size variation · *Ambystoma macrodactylum*

Introduction

Cannibalism can have very different functions depending on whether its effects are considered at the level of the individual or the population. By consuming conspecifics, individual cannibals may enjoy a number of benefits including enhanced growth (Nagai et al. 1971; Meffe and Crump 1987; Crump 1990; Wildy et al. 1998) and the elimination of conspecific competitors for heterospecific prey items (Fox 1975; Polis 1981; Crump 1983). In addition, long-term exposure to cannibals may influence the development of antipredator behavior in potential conspecific prey (Holomuzki 1986; Kats et al. 1988; Chivers et al. 1997; Wildy et al. 1999).

Cannibalism (i.e. intraspecific predation), like interspecific predator-prey interactions, can also have important implications for the regulation of population structure and dynamics (Fox 1975; Polis 1981; Dong and Polis 1992). Depending on the frequency with which it occurs, cannibalism may function to regulate a population through its effects on the spread of disease (Polis 1981; Pfennig et al. 1991, 1998) and the alteration of population size (Polis 1981; Ziemba and Collins 1999), size structure (Ziemba and Collins 1999) and age structure (Fox 1975; Stevens 1992). Although it is important to examine the implications of cannibalism, to fully understand these effects, the environmental factors influencing this behavior must also be identified.

Intraspecific aggression in animals can be influenced by a variety of factors including competition for food (Persson 1988; Drummond and Chavelas 1989), mates (Ovaska 1987), and space (Crowley et al. 1987; Ducey and Ritsema 1988; Mathis 1990; Walls 1990). Intraspecific aggression, including cannibalism, has been docu-

E.L. Wildy (✉)
Department of Biological Sciences,
California State University, 25800 Carlos Bee Boulevard,
Hayward, California, 94542–3090, USA
e-mail: ewildy@bay.csu Hayward.edu
Tel.: +1-510-8854387, Fax: +1-510-8854747

D.P. Chivers
Department of Biology, University of Saskatchewan,
112 Science Place, Saskatoon, SK, S7 N 5E2 Canada

J.M. Kiesecker
Department of Biology, Pennsylvania State University,
208 Mueller Lab, University Park, PA 16802, USA

A.R. Blaustein
Department of Zoology, Oregon State University, Corvallis,
OR 97331, USA

mented in numerous amphibian species (see reviews in Fox 1975; Polis 1981; Polis and Meyers, 1985; Crump 1992; Mathis et al. 1994). In amphibians, aggressive behaviors (including cannibalism) may also be influenced by the presence of vulnerable heterospecific (Maret and Collins 1996) or conspecific prey (Loeb et al. 1994; Maret and Collins, 1994), diet type (Pfennig 1990; Walls 1993b), the presence of kin (Pfennig and Collins 1993; Walls and Blaustein 1995; Pfennig and Frankino 1997; Pfennig 1999), food limitation (Semlitsch and Reichling 1989; Walls 1998), and conspecific density (Collins and Cheek 1983; Semlitsch and Reichling 1989; Walls 1998).

Variation in conspecific density and food limitation has been associated with increased aggression in amphibians and in the development of morphologies that serve as indicators of aggressive behavior (i.e. cannibalistic morphologies) at both the aquatic (Fox 1975; Polis 1981; Collins and Cheek 1983; Crump 1983; Semlitsch and Reichling 1989) and terrestrial (Ducey and Heuer 1991) life history stages. Furthermore, increased size variation among individuals within a population may promote agonistic interactions within populations of larval amphibians (Maret and Collins 1994; Ziemba and Collins 1999). It has been suggested that in populations with high size variation, smaller individuals are more vulnerable to aggression from larger conspecifics (Fox 1975; Polis 1981; Dong and Polis 1992). This situation may be further aggravated by other factors including high densities of conspecifics and/or low food resources.

Agonistic behaviors, in the form of intraspecific biting and cannibalism, have been documented in populations of larval long-toed salamanders, *Ambystoma macrodactylum*, (Anderson 1967; Nussbaum et al. 1983; Walls et al. 1993a, b; Wildy et al. 1998, 1999). Cannibalism, in particular, has been documented in populations of this species living in ephemeral habitats (Walls et al. 1993a; Wildy et al., 1998), where densities of larvae can gradually increase and per capita food resources can become limited as pond drying occurs (Wildy, personal observation). Furthermore, larvae within these populations can exhibit high variance in body size. In this study, we examined how density and food availability affect size variation within a population and how this may, in turn, influence aggression among individuals within that population.

Materials and methods

We collected larvae that were approximately 1 month post hatching in February 1996 from an ephemeral pond located approximately 26 km east of Corvallis, Benton County, Oregon, USA. We transported larvae to the laboratory and housed them in four 38-l aquaria. These larvae served as our source group. Prior to the experiment, larvae were fed zooplankton ad libitum every other day and were maintained on a 14:10 h light:dark cycle.

Our experiment began on 12 March 1996 and involved a 2x2 factorial design, crossing two levels of density with two levels of food. Larvae were raised in 38-l aquaria in one of four treatments: (1) low density/low food (2) low density/high food (3) high density/low food and (4) high density/high food. Initially, each treatment was replicated six times for a total of 24 aquaria. However, one aquarium in the low density/low food treatment was eliminated from the analysis due to the unexplained death of all of the larvae within. Our final analysis included 23 aquaria. Focal larvae were chosen from the four source aquaria. Individuals were visually matched for size so that initial differences in size would be minimal.

Density regimes consisted of 10 larvae and 40 larvae for the low and high levels, respectively. For the first 4 weeks, all larvae were fed zooplankton collected from local ponds every other day. Animals in the low food treatments were given 2 ml of a solution of zooplankton per larva for a total of 20 ml in the low density/low food treatments and 80ml in the high density/low food treatments. Animals in the high food treatments were given 8 ml of the solution per larva for a total of 80ml in the low density/high food treatments and 320 ml in the high density/high food treatments. To provide a standard density of zooplankton in each aliquot, we thoroughly stirred the zooplankton solution before each aliquot was extracted. After week 5, as larvae grew, they were fed *Tubifex* worms every other day. Larvae received 10 worms or 40 worms total in the low density/low food and high density/low food treatments respectively (i.e. 1 worm per larva) and 40 worms or 160 worms in the high density/low food and high density/high food treatments, respectively (i.e. 4 worms per larva).

We monitored the experimental aquaria daily and removed the bodies of larvae that had died. A weekly assessment of the total number of larvae within each aquarium was conducted. Larvae that were missing and could not be accounted for due to metamorphosis or because they had died and had been removed were presumed to have been cannibalized. Aquaria were cleaned once per week during which time all larvae were removed. During weeks 3, 5, 7 and 9, as larvae were removed from their aquaria, they were assessed for injuries due to intraspecific biting. Larvae were considered to be recipients of a bite(s) if they exhibited damage to their limbs, tail and/or gills. We chose to assess these particular characters because they are common sites of damage resulting from conspecific attack in larval salamanders (Semlitsch and Reichling 1989; Wildy et al., personal observation). Measurements were repeated every other week as opposed to every week, because it allowed time for larvae to initiate regeneration of missing pieces of tail, limbs or gills making it easier for the observer to differentiate between old and new wounds. As test animals reached metamorphosis (i.e. beginning of gill reabsorption) they were removed from their aquarium and their snout-vent length was recorded and time to metamorphosis, in days, was calculated.

The experiment ended after 100 days (19 June 1996), an amount of time which falls within normal ranges of pond duration inhabited by this species in this region (Wildy et al., personal observation). Larvae that had not completed metamorphosis at this time were considered to have not survived.

Statistical analysis

For all analyses, parametric assumptions were met and, therefore, no data transformations were performed. Multivariate analysis of variance (MANOVA) was used to examine the effects of density and food level on survival, time to and size at metamorphosis of the test animals. After MANOVA, univariate analysis of variance (ANOVA) *F* tests were used on each response variable to assess which variables were responsible for significant main effects. For each response variable, we calculated tank means for the animals in each tank and used these means for all statistical analyses. Post hoc comparisons (Tukey tests) were used to check for differences between means for the four treatments.

Measurements of total (i.e. averaged over weeks 3, 5, 7 and 9) within-tank variation in snout-vent length, total biting and total cannibalism were analyzed using ANOVAs. As a measure of variation in larval size, the coefficient of variation (CV) of within-tank snout-vent length was calculated and averaged across tanks. To assess biting, we averaged the total number of injuries received by

each larva throughout the duration of the experiment and averaged the number of injuries per tank. At the end of each 2-week period, the level of cannibalism within a tank was assessed by calculating the percentage of larvae that were missing and therefore, presumed eaten. We used repeated measures ANOVAs to evaluate the effects of density and food level on these three response variables over time. Tank means for all three measurements were used for all statistical analyses. Finally, the correlative relationships between CV in size, intraspecific biting and cannibalism were examined using the Pearson product moment correlation.

Results

The results of our ANOVA indicated that larvae responded differently with respect to the coefficient of variation (CV) in size, biting, and cannibalism depending on the levels of density and food at which they were reared (Tables 1, 2, 3). Total CV in size, biting, and can-

Table 1 Summary statistics for ANOVA of total coefficient of variation (CV) in snout-vent length over weeks 3, 5, 7 and 9 and for repeated-measures ANOVA for coefficient of variation

Source of variation	<i>F</i>	<i>df</i>	<i>P</i>
Total CV			
Density	2.898	1	0.105
Food	10.142	1	0.005
Density × food	0.640	1	0.434
CV over time			
Between-subject effects			
Density	2.890	1	0.105
Food	10.156	1	0.005
Density × food	0.636	1	0.435
Within-subject effects			
Time	20.620	3	0.000
Time × density	5.498	3	0.002
Time × food	4.623	3	0.006
Time × density × food	0.486	3	0.693

Table 2 Summary statistics for ANOVA of total aggression over weeks 3, 5, 7, and 9 and for repeated-measures ANOVA for aggression

Source of variation	<i>F</i>	<i>df</i>	<i>P</i>
Total aggression			
Density	0.571	1	0.459
Food	26.044	1	0.000
Density × food	2.940	1	0.103
Aggression over time			
Between-subject effects			
Density	0.570	1	0.459
Food	26.039	1	0.000
Density × food	2.940	1	0.103
Within-subject effects			
Time	22.606	3	0.000
Time × density	7.861	3	0.000
Time × food	21.445	3	0.000
Time × density × food	3.725	3	0.016

nibalism were all highest in the two low food treatments (Fig. 1). Density did not influence total CV in size or total aggression observed (Tables 1, 2; Fig. 1a, b) (although our power for these tests was low and may have resulted in a type II error in this case: total CV=0.244, $\alpha=0.05$; total aggression =0.05, $\alpha=0.05$). However, differences in density at which larvae were reared did influence the average amount of cannibalism exhibited amongst larval groups throughout the experiment (Table 3, Fig. 1c).

The effects of density and food on within-tank size variation, biting and cannibalism appeared to change over time (Tables 1, 2, 3). In addition, significant interactions between time and density and time and food were found for CV in size and cannibalism (Tables 1, 3). Significant interactions between time and density, time and food and time, density and food were found for biting (Table 2). During the first half of the study (i.e. weeks 3 and 5), size variation was the highest in the high density/low food treatment followed by the high density/high food, low density/low food and low density/low food treatments (Fig. 2a). During this same period, larvae in both high density treatments and in the low density/low food treatment exhibited the greatest amount of biting (Fig. 2b). However, during the latter half of the study (i.e. weeks 7 and 9), low food availability appeared to be most important in influencing an increase in both size variation and biting among larvae (Fig. 2b). Cannibalism occurred with the greatest frequency at the beginning of the experiment (i.e. week 3) in the high density/low food treatment followed by the low density/low food and high density/high food treatments (Fig. 2c).

The correlative relationships between size variation, biting and cannibalism were examined. Size variation was found to be highly positively correlated with cannibalism (Pearson correlation coefficient =0.666; $P=0.0005$) and only slightly with intraspecific biting (Pearson correlation

Table 3 Summary statistics for ANOVA for total cannibalism over weeks 3, 5, 7, and 9 and for repeated-measures ANOVA for cannibalism

Source of variation	<i>F</i>	<i>df</i>	<i>P</i>
Total cannibalism			
Density	17.699	1	0.000
Food	60.711	1	0.000
Density × food	2.177	1	0.156
Cannibalism over time			
Between-subject effects			
Density	17.775	1	0.000
Food	61.138	1	0.000
Density × food	2.137	1	0.160
Within-subject effects			
Time	40.356	3	0.000
Time × density	6.691	3	0.001
Time × food	4.961	3	0.007
Time × density × food	3.725	3	0.365

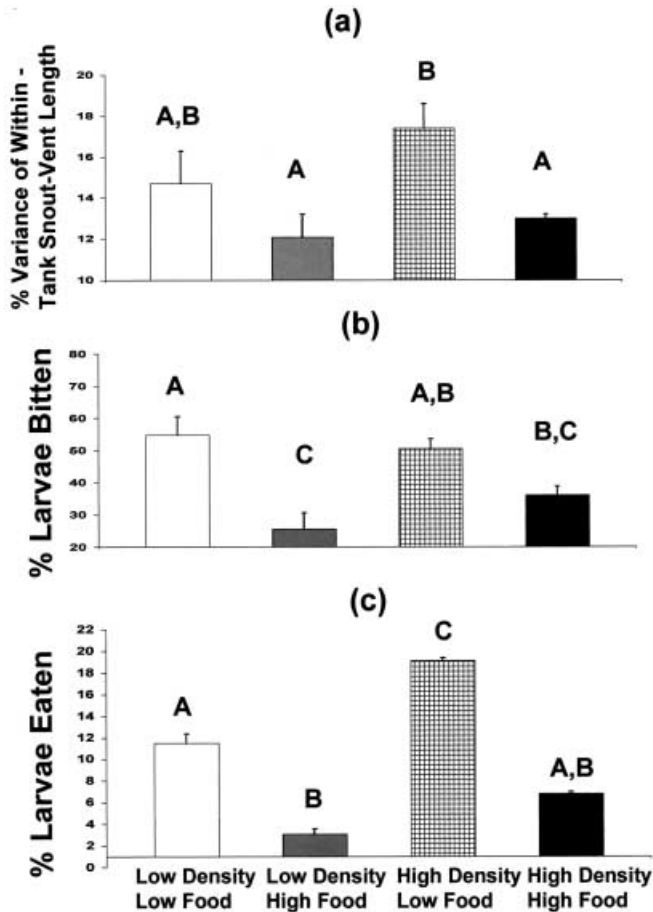


Fig. 1 Mean ($\pm$ SE) **a** coefficient of variation of snout-vent length, **b** aggression (percent larvae bitten) and **c** cannibalism (percent larvae eaten) for *Ambystoma macrodactylum* larvae exposed to low and/or high density and food levels. All data represent averages of measurements taken during weeks 3, 5, 7 and 9. If two treatments share the same letter, there is no significant difference between them

coefficient = 0.320; $P=0.136$). Moreover, total aggression and cannibalism were highly correlated (Pearson correlation coefficient = 0.672; $P=0.0004$).

The results of our MANOVA revealed strong main effects of density and food on larval life history (Table 4). In addition, there was a strong interaction between density and food level. Post hoc ANOVAs indicated larval survival and the time required to reach metamorphosis were affected by both food level and density (Table 4). Larvae exhibited reduced survival and took longer to metamorphose in the two low food treatments (Fig. 3a, b). Higher densities appeared to reduce the time it took for larvae to metamorphose within low food treatments and decreased the probability of survival within both low and high food treatments (Fig. 3a, b).

Size at metamorphosis was slightly influenced by food levels such that larvae in the most benign treatment, low density/high food, exhibited the greatest mean snout-vent length ($SVL \pm SE = 30.23 \pm 0.52$) by the end of the experiment (Fig. 3c).

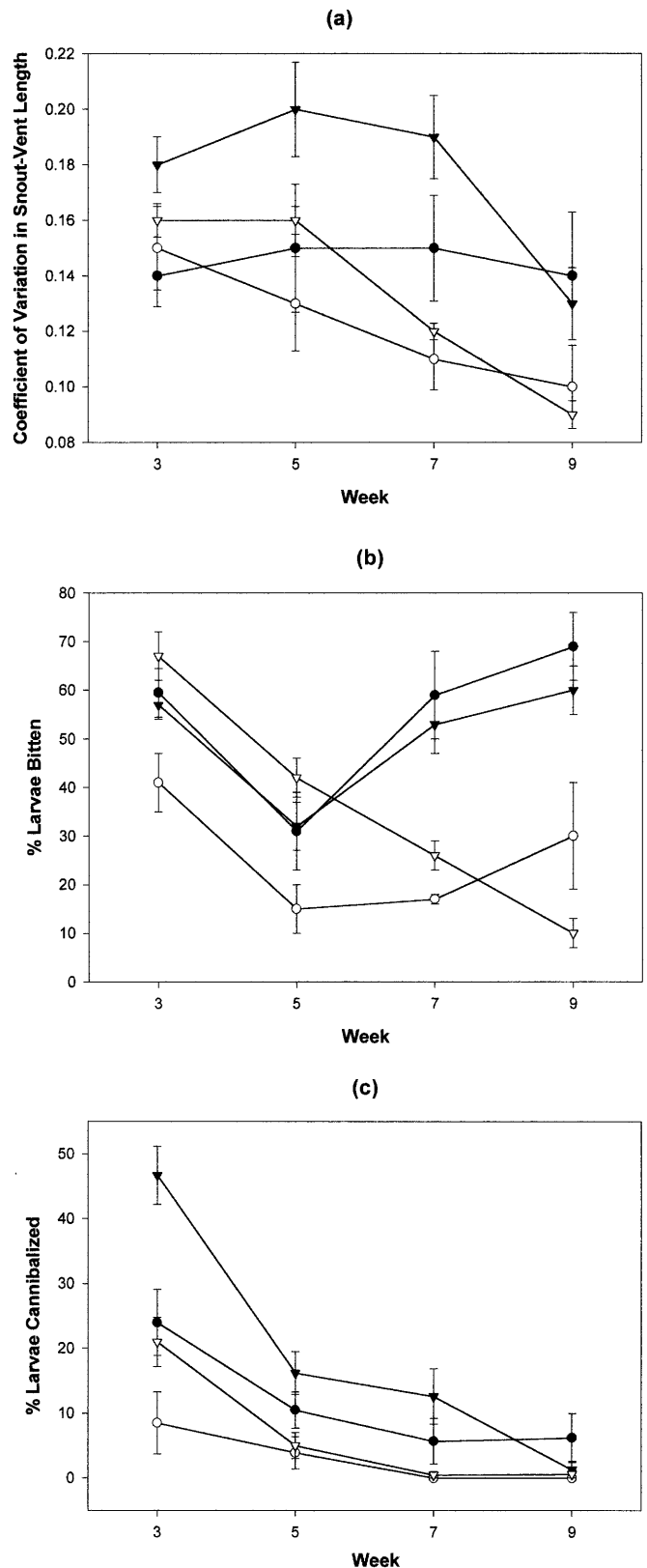


Fig. 2 Change in **a** coefficient of variation (CV) in body size, **b** aggression and **c** cannibalism over time for *A. macrodactylum* larvae raised in the low density/low food ($\bullet$), low density/high food ($\circ$), high density/low food ($\blacktriangle$) and high density/high food ($\triangle$) treatments

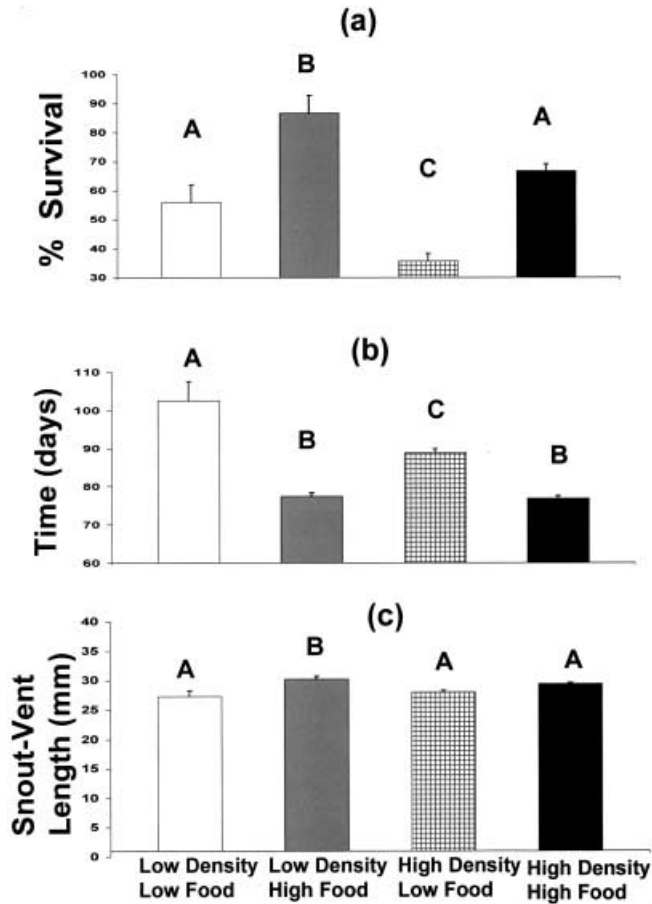


Fig. 3 Mean ($\pm$ SE) **a** percent survival to, **b** time to (days) and **c** size (millimeters) at metamorphosis for *A. macrodactylum* larvae exposed to low and/or high density and food levels. Letters over bars indicate which treatments are statistically different from one another. If two treatments share the same letter, there is no significant difference between them

Discussion

Our results indicate that variation in density and food level can influence agonistic behavior within groups of larval *A. macrodactylum*. We found a strong effect of food level on both intraspecific biting and cannibalism. Hunger levels for larvae reared at low food levels were presumably higher than for larvae raised in the high food treatments. Consequently, biting was heightened in these treatments. In addition, we found that within a given food treatment, cannibalism occurred with greater frequency at higher densities. In fact, the highest frequency of cannibalism was recorded for larvae reared in the high density/low food treatment. An increase in the incidence of cannibalism was observed in the low density/low food and high density/high food treatments relative to the low density/high food treatments, but not to the same degree as in the high density/low food treatment. This may be explained by the potential costs associated with engaging in that behavior. The potential costs to a cannibal can include injury resulting from struggling with a potential

Table 4 Results of MANOVA for overall effects of food level and density on time to, survival to and size at metamorphosis for larval *Ambystoma macrodactylum* and ANOVAs for each response variable

	<i>F</i>	<i>df</i>	<i>P</i>
MANOVA			
Constant	9,040.794	3, 17	0.000
Density	9.978	3, 17	0.001
Food	171.513	3, 17	0.000
Density $\times$ food	9.259	3, 17	0.001
ANOVAs			
Survival			
Density	19.837	1, 19	0.000
Food	46.506	1, 19	0.000
Density $\times$ food	0.000	1, 19	0.985
Time			
Density	9.584	1, 19	0.006
Food	65.305	1, 19	0.000
Density $\times$ food	8.154	1, 19	0.010
Mass			
Density	0.001	1, 19	0.971
Food	17.546	1, 19	0.000
Density $\times$ food	2.123	1, 19	0.161

victim (Crump 1992; Dong and Polis 1992), the inadvertent consumption of a relative (Dong and Polis 1992) or increased exposure to disease (Polis 1981; Pfennig et al. 1991, 1998; but see Pfennig et al. 1999). These risks may have prevented cannibalism from occurring with even higher frequency in the low density/low food and high density/high food treatments, which may be considered less extreme environments relative to the high density/low food treatment. However, under more extreme environmental conditions, the benefits of cannibalism should begin to outweigh the costs. For example, for larvae reared with a high density of conspecifics and low food levels, there is increased competition for limited food. Under these circumstances, becoming a cannibal may be very adaptive for a larva for several reasons. First, locating (conspecific) prey under these conditions would not be difficult as the encounter rate between larvae would be high. Furthermore, in consuming a conspecific, a larva decreases its probability of starvation, reduces its competition for any remaining food items, and increases per capita food.

We suggest that the pattern of larval survival in the different treatments can be explained directly through the effects that food level and density had on larval health and indirectly through the influence that these factors had on intra-group aggression. Larvae in the two low food treatments exhibited reduced survival compared to animals in the high food treatments. Moreover, within a food treatment, larvae raised at higher densities did not survive as well. In the low food treatments, competition for food was presumably higher, particularly in the high density/low food treatments. Consequently, it is likely that some animals did not consume an adequate

amount of food and grew weaker and weaker throughout the experiment. This alone may have contributed to decreased survival in these treatments. However, it is very likely that variation in food and density at which larvae were reared indirectly affected survival through direct effects that these two factors had on aggression. Biting was heightened in the low food treatments. Injuries from being bitten (Semlitsch and Reichling 1989) combined with weakness due to low food intake could explain reduced survival among larvae observed in these treatments. Furthermore, increased cannibalism, particularly in the two low food treatments, but also in the high density/high food treatments, likely contributed to low survival in those treatments.

In the current study, we found a strong effect of low food availability as well as high conspecific density on increased aggression. Only a few studies have demonstrated a correlation between decreased food availability and increased aggression in amphibians (Ducey and Heuer 1991). This is surprising since limited food resources have been documented in nature for larval amphibian populations (Petranka 1984; Petranka and Sih 1986; Scott 1990).

Many more studies suggest that density is the principal factor affecting aggression and cannibalism (e.g. Collins and Cheek 1983; Semlitsch and Reichling 1989; Nishihara 1996). For example, Semlitsch and Reichling (1989) found an effect of higher densities and constant water levels on aggression in larval mole salamanders (*A. talpoideum*) and an inverse relationship between density and larval injury and survival (due to cannibalism and/or vulnerability due to the effects of injury). However, they found no relationship between food level and larval injury or survival. Collins and Cheek (1983) manipulated food level and conspecific density and found that high density, but not low food levels, influenced the production of cannibal morphs in larval Arizona tiger salamanders (*A. t. nebulosum*).

In some studies, the effects of conspecific density on specific biotic responses are often explained in light of the indirect effects of density on available food resources. Per capita food typically becomes limited at higher densities (i.e. Dash and Hota 1980; Smith 1983; Newman 1987; Maret and Collins 1994). Thus, higher density coupled with limited food resources may influence the intensity of competition between conspecifics (Semlitsch 1987; Maret and Collins 1994) which may, in turn, heighten intraspecific aggression amongst individuals (Maret and Collins 1994). In the current study, we manipulated both density and food separately and found that manipulation of food availability alone can influence agonistic behaviors directly, through its effects on hunger levels. In addition, food limitation may promote biting and cannibalism indirectly through the promotion of increased group size variation.

An increase in size variation within larval groups may have facilitated increased incidences of biting and cannibalism in some treatments. Variation in size within a population of larval amphibians does exist naturally and

may occur for several reasons. For example, size differences may be the result of genetic differences between clutches. Alternatively, larvae that are of similar size initially may engage in unequal acquisition of food by chance or due to differences in patterns of resource use, allowing some individuals to become larger faster.

We believe that this latter scenario occurred in our study. At the beginning of the experiment, larvae were all approximately the same size. Therefore, variation in larval size occurring during the experiment could only have been the result of genetic differences or unequal food acquisition by larvae within a tank. We can effectively rule out genetic differences since larvae were randomly assigned both to a treatment and to a particular aquarium within that treatment. Therefore variation in size observed was likely the result of some larvae consuming more food than others over time. This conclusion is further supported by our finding that differences in group size variation were attributed to a food effect but not a density effect. Some larvae apparently consumed disproportionately more resources than others causing a significant divergence in size among individuals by the end of the experiment. The growth advantage gained by these larvae could have allowed these individuals to retain a size-dependent competitive advantage throughout the rest of the larval period (Persson 1985; Smith 1990; Walls and Semlitsch 1991).

We suspect that larger individuals, driven by hunger, were the primary aggressors in our study and that they initiated agonistic interactions. Those individuals cannibalizing conspecifics presumably enjoyed enhanced growth that may have further contributed to the divergence of size among larvae.

Larvae in the low food treatments took longer to metamorphose. In addition, some individuals did not metamorphose at all and were considered to have not survived. These patterns can likely be explained by the reduced growth potential of smaller larvae whose foraging efforts were compromised (Smith 1990) perhaps due to being attacked by larger animals (Van Buskirk and Smith 1991; Ziemba and Collins 1999) and/or due to changes in their foraging patterns (Holomuzki 1986; Chivers et al. 1997; Ziemba and Collins 1999) and activity (Chivers et al. 1997; Wildy et al. 1999) in response to the presence of these larger, more aggressive conspecifics. However, we did not actually qualify whether larger or smaller animals were initiating agonistic interactions during the experiment. Therefore, it is possible low food availability increased aggression amongst all larvae regardless of their size relative to other larvae in the same tank.

The influence of size variation on aggression in amphibians has been demonstrated in only a few studies. For example, Maret and Collins (1994) showed that cannibalistic larval Arizona tiger salamanders (*Ambystoma tigrinum nebulosum*) developed under conditions where size variation was high and they were one of the largest animals in a group of conspecifics. They suggested that larval Arizona tiger salamanders may use an assessment

of their size relative to surrounding conspecifics as a guide with which they may determine their success as a cannibal. Several other studies have suggested that size variation is important in influencing aggression (e.g. Kusano et al. 1985; Nyman et al. 1993; Maret and Collins 1994; Petranksa and Thomas 1995; but see Pfennig and Collins 1993; Pfennig and Frankino 1997; but see Brunkow and Collins 1998).

The interaction between density, food level, and size variation has also been previously explored. Walls (1998) showed that food limitation can play a significant role in influencing variation in size but not aggression in larval spotted salamanders (*A. maculatum*). The size ratio between largest and smallest larva within a tank, which she suggested to be an indicator of the potential for cannibalism, was affected by density and food level treatments in which they were raised. Size ratio between largest and smallest individuals and proportion of individuals cannibalized was highest in high density treatments but food supplementation significantly reduced the amount of cannibalism within these treatments. She found no differences in larval aggression between the three treatments. Furthermore, she concluded that density-dependent growth in her study was more likely the result of food limitation than of interference competition.

Our study revealed that groups of larvae raised at low food levels exhibited high size variation. Moreover, the amount of size variation within groups of larvae was highly positively correlated with the amount of cannibalism exhibited within those same groups. The amount of cannibalism was, in turn, highly correlated with the amount of intraspecific biting observed. We suggest that biting, a less extreme form of aggression, can be viewed as a precursor to cannibalism, a more extreme form of aggression. Furthermore, we suggest that the degree of aggression exhibited by larvae depends on the harshness of the environment. To our knowledge, this is one of the first studies to experimentally demonstrate a relationship between low food levels and high conspecific densities with increased size variation and increased aggression in larval amphibians.

Acknowledgements We would like to thank S. Gerard, R. Kimble, M.D and O.A. Man for assistance in collection and maintenance of animals during the experiment. In addition we like to mention our appreciation to Susan Walls who provided aid on project design and to Lisa Belden, Audrey Hatch and Eric Hoffman who provided us with statistical advice and to Lisa, Audrey, Eric and two anonymous reviewers for their helpful comments on an earlier version of this manuscript. This study was supported by Oregon State University, Department of Zoology Research Funds, Sigma Xi, Animal Behavior Society Research Award funds, the Natural Sciences and Engineering Research Council of Canada and the National Science Foundation (Grant DEB 9423333).

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