

SHIFTS IN LIFE-HISTORY TRAITS AS A RESPONSE TO
CANNIBALISM IN LARVAL LONG-TOED
SALAMANDERS (*Ambystoma macrodactylum*)

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Abstract—We examined the potential influence of cannibalism on life-history characteristics of larval long-toed salamanders (*Ambystoma macrodactylum*). Using a 2 × 2 factorial design, crossing morphology with diet, we exposed typical morph larvae to one of four types of stimulus animals: cannibal morphs fed a conspecific diet, cannibal morphs fed a heterospecific diet (i.e., *Tubifex*), typical morphs fed a conspecific diet, and typical morphs fed a heterospecific diet. Test larvae exposed to stimulus animals fed a conspecific diet exhibited a slower growth rate and an increase in the time taken to reach metamorphosis. These changes in life history likely represent a cost of antipredator behavior.

Key Words—*Ambystoma macrodactylum*, long-toed salamander, cannibal morphology, cannibalism, life history traits, antipredatory behavior, chemical cues, polymorphism.

INTRODUCTION

A wide diversity of antipredator responses has evolved among prey animals. These antipredatory mechanisms can include changes in morphology (e.g., Havel and Dodson, 1984; Havel, 1987; Brönmark and Miner, 1992; McCollum and Van Buskirk, 1996; Stabell and Lwin, 1997), physiology (e.g., Wassersug, 1971;

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Smith, 1982), and behavior (e.g., Lima and Dill, 1990; Chivers et al., 1996, 1997). Behavioral responses to predators may include an increase in the use of shelter, shifts in microhabitat use, reductions in movement, and increased group cohesion (Sih, 1987; Lima and Dill, 1990; Chivers and Smith, 1998; Kats and Dill, 1998). For example, Sih (1986) found that mosquito larvae (*Culex pipiens*) reduce their activity when exposed to the insect predator *Notonecta undulata*. Alternatively, Chivers et al. (1995) found that brook stickleback increased schooling in response to the presence of predatory northern pike. Although each of these behaviors may shield an individual from predation, a trade-off commonly arises between avoiding a predator and performing other activities, including foraging (Sih, 1992). This trade-off can lead to a variety of indirect effects on long-term life-history traits of the prey.

There are many studies in which long-term effects of predators on their potential prey have been documented (e.g., Minchella and Loverde, 1981; Werner et al., 1983; Dodson and Havel, 1988; Reznick et al., 1990; Wilbur and Fauth, 1990; Skelly, 1992; Ball and Baker, 1996). Werner et al. (1983) found that the presence of predatory largemouth bass (*Micropterus salmoides*) led to a decrease in the growth rate of small bluegill sunfish (*Leopomis macrochirus*). A study of Dodson and Havel (1988) indicated that *Daphnia pulex* exposed to the nonlethal presence of the invertebrate predator, *Notonecta undulata*, exhibited a reduction in adult body size and a shorter developmental time in juveniles. Skelly (1992) showed that gray treefrog (*Hyla versicolor*) tadpoles exposed to the nonlethal presence of larval tiger salamanders (*Ambystoma tigrinum*) experienced a reduction in their growth and developmental rate. Other examples of long-term effects of predators on amphibian life history are provided by Van Buskirk (1988), Wilbur and Fauth (1990), and Skelly and Werner (1990).

Intraspecific predation (cannibalism) is common in numerous taxa, including amphibians (Fox, 1975; Polis, 1981; Smith and Reay, 1991; Crump, 1992; Elgar and Crespi, 1992; Wildy et al., 1998). Despite the widespread occurrence of cannibalism, there is little information on how intraspecific predation influences long-term life-history traits of conspecific prey. In this study we explored the possibility that cues of cannibalistic conspecifics may influence life-history characteristics of larval long-toed salamanders (*Ambystoma macrodactylum*). Larvae of this species exhibit a trophic polymorphism, whereby some individuals have a cannibalistic morphology (i.e., a disproportionately large head and hypertrophied vomerine teeth) (Walls et al., 1993a,b). Larvae lacking cannibalistic characteristics are referred to as typical morphs.

Chivers et al. (1997) documented that typical morph *A. macrodactylum* larvae responded to chemical cues but not visual cues of cannibal morphs with antipredator behavior. Specifically, typical morphs spatially avoided cannibals and showed a reduction in activity in their presence. In this experiment, we used larval *A. macrodactylum* as both predator and prey and tested whether the mor-

phology of the predator, its diet type (i.e., conspecifics or heterospecifics), or an interaction between the two, influence long-term life history characteristics of their conspecific prey. Specifically, we looked at how growth rate, time taken to reach metamorphosis, and mass at metamorphosis are influenced by intraspecific predators.

METHODS AND MATERIALS

We collected long-toed salamander larvae in July 1996 from a high-altitude (elevation 1951 m) ephemeral pond located approximately 24 km south of Sisters, Deschutes County, Oregon, USA. We transported them to the laboratory and housed individual larvae in 850-ml plastic cups containing approximately 600 ml of dechlorinated tap water. Prior to the experiment, larvae were fed *Tubifex* ad libitum every other day and were maintained on a 14L:10D cycle.

We created experimental chambers using fiberglass mesh screen to divide glass test aquaria (50 × 25 × 30 cm) into five sections. A central area, measuring 10 × 25 cm was surrounded by four sections each measuring 12.5 × 20 cm. Within these aquaria, we raised typical morph larvae in the presence of one of four types of stimulus animals: (1) cannibal morphs fed a conspecific diet, (2) cannibal morphs fed a heterospecific diet (i.e., *Tubifex*), (3) typical morphs fed a conspecific diet, and (4) typical morphs fed a heterospecific diet. [We used the criteria of Walls et al. (1993a,b) to identify individuals with the typical and cannibal morphology]. Within each aquarium, a single typical morph test larva was placed in each of the four peripheral sections. Depending on the treatment, one of the four types of stimulus larvae was placed in the central section.

Aquaria were arranged in blocks with each block containing one of the four treatment types. This design was replicated seven times for a total of 112 animals housed in 28 aquaria. Within each block, both the stimulus animals (cannibal morphs and typical morphs) and the test animals were matched for size. The mean mass and standard error of the stimulus animals was 33.2 ± 1.3 g, while that of the test animals was 26.6 ± 2.0 g.

Throughout the experiment, test larvae were fed *Tubifex* ad libitum every other day. Stimulus animals were fed ad libitum twice per week with either *Tubifex* or larval *A. macrodactylum*. (Feeder larvae were always smaller than stimulus larvae.) Aquaria were cleaned once per week. Aquaria were initially filled to a depth of 27.5 cm. Beginning at week 6, the water level in the tanks was lowered by 2.5 cm/week to simulate natural pond drying. We began dropping the water level prior to metamorphosis of any test larvae.

We monitored the experimental aquaria daily. All test animals that reached metamorphosis (i.e., beginning of gill resorption) were removed from the test chambers and weighed. If a stimulus animal transformed prior to the end of

the experiment, we replaced it with another stimulus animal that was the same size and had the same morphology and diet. For each test animal, we calculated growth rate by dividing the difference between initial and final mass by the number of days from the beginning of the experiment to metamorphosis. For each response variable (see below), we calculated tank means for the four animals in each tank and used these means for all statistical analyses.

Our data conformed to assumptions of parametric statistics. Therefore, we used a multivariate analysis of variance (MANOVA) to examine the effects of morphology and diet of the stimulus animals on life-history traits of the test animals. After MANOVA, we used univariate analysis of variance (ANOVA) on each response variable to assess which variables were responsible for significant main effects.

RESULTS

MANOVA revealed that there was an overall effect of the treatment conditions on the life history variables that we measured (see Table 1). Subsequent ANOVAs showed that growth rate and time taken to reach metamorphosis, but not mass at metamorphosis, were influenced by the diet of the stimulus animals (Table 1, Figure 1). Neither growth rate, time taken to reach metamorphosis, nor mass at metamorphosis was influenced by the morphology of the stimulus animals (Table 1, Figure 1). There were no significant interactions between morphology and diet (Table 1, Figure 1).

DISCUSSION

Larval long-toed salamanders exhibited significant changes in life-history characteristics in response to conspecifics that had cannibalized. Larvae exhibited a significantly slower growth rate and an increased time taken to reach metamorphosis when exposed to cues from stimulus animals fed a diet of conspecifics as opposed to heterospecifics.

Previous studies support the idea that the diet of a potential predator can influence both short-term and long-term responses in potential prey (see reviews in Chivers and Smith, 1998; and Kats and Dill, 1998). For example, Wilson and Lefcort (1993) found that red-legged frog tadpoles reduced activity when exposed to chemical cues from newts fed a diet of red-legged frog tadpoles but not when they were fed insects. A more long-term response was demonstrated by Crowl and Covich (1990), who showed that stream snails (*Physella virgata*) exhibited faster growth and a delay in reproduction in response to cues from predatory crayfish feeding on other stream snails. In our study, we show that larval *A. macrodactylum* experience an increased time to metamorphosis and

TABLE 1. RESULTS OF MANOVA FOR OVERALL EFFECTS OF STIMULUS TYPES (DIET AND MORPHOLOGY) ON LIFE-HISTORY TRAITS AND ANOVAs FOR EACH RESPONSE VARIABLE^a

Source	F	P
MANOVA		
Constant	4418.57	<0.001
Diet	26.827	<0.001
Morph	1.926	0.166
Diet × morphology	0.801	0.301
ANOVAs		
Rate		
Diet	15.550	<0.001
Morphology	0.149	0.704
Diet × morphology	0.075	0.787
Time		
Diet	25.239	<0.001
Morphology	2.976	0.102
Diet × morphology	3.006	0.100
Mass		
Diet	2.024	0.172
Morphology	0.009	0.925
Diet × morphology	2.162	0.159

^aResponse variables are growth rate (rate), time taken to reach metamorphosis (time), and mass at metamorphosis (mass). Degrees of freedom are 3, 16 for MANOVAs and 1, 18 for ANOVAs.

a decreased growth rate when exposed to other larval *A. macrodactylum* that have been fed a diet of conspecifics but not when they have been fed a diet of *Tubifex*. These results are particularly interesting because predator and prey belong to the same species. In noncannibalistic populations, conspecifics may engage in competitive and/or reproductive interactions. For cannibalistic populations, predator-prey interactions may also be important.

In our study, there was no effect of the morphology of the stimulus animals on any of the life history variables that we measured. Test animals responded to the stimulus animals in the same manner, regardless of whether or not the stimulus animals had a cannibal morphology. These results differ somewhat from our past behavioral studies (Chivers et al., 1997).

Previously we found that typical morph long-toed salamander larvae exhibited antipredatory behavior in response to chemical cues of conspecific stimulus animals possessing a cannibalistic morphology. This response occurred not only when the cannibal morphs were fed a conspecific diet (as in the present study) but also when they were fed *Tubifex*. The differences in conclusions between the two experiments deserves consideration. We believe that the differences can be explained in the following way: In the behavioral experiments, the typical larvae exhibited an immediate behavioral response when presented with a predatory

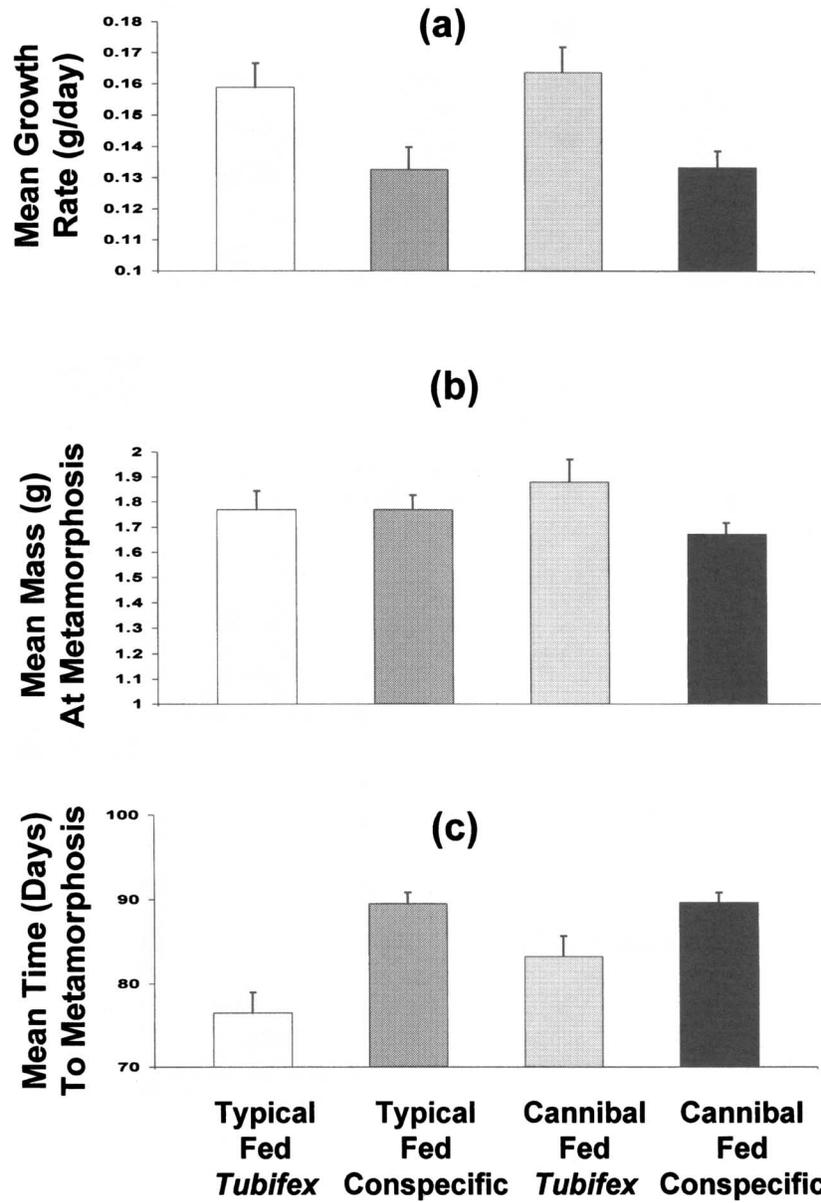


FIG. 1. (a) Mean (\pm SE) growth rate (grams per day) for *A. macrodactylum* test larvae, (b) Mean (\pm SE) mass (grams) at metamorphosis, (c) mean (\pm SE) time (days) to metamorphosis.

threat from a cannibal. In this instance, we only observed the behavior of the test animals for a short duration (20 min). Theory predicts that the antipredator response of the test animals to the cannibal should diminish over time if the cannibal does not attack (Lima and Dill, 1990). In the present experiment, the test animals had a long period of time to assess the potential risk posed by the cannibal. In this case, the test animals responded to the cannibals only when the cannibals acted cannibalistic (i.e., when they had consumed a conspecific diet). This interpretation is supported by examining the responses of test larvae to typical morph stimulus animals. Test animals responded to typical morph stimulus animals when the stimulus animals acted cannibalistic (i.e., had a conspecific diet), but not when the stimulus animals did not (i.e. had a *Tubifex* diet).

Long-term life-history shifts may result as by-products of antipredatory behavior (e.g., Dodson and Havel, 1988; Skelly and Werner, 1990; Skelly, 1992; Ball and Baker, 1996) or may represent facultative alterations in life history (e.g., Minchella and Loverde, 1981; Crowl and Covich, 1990; Wilbur and Fauth, 1990) or a combination of both (e.g., Skelly and Werner, 1990). We suspect that the differences in life-history traits that we observed may be a consequence or by-product of the behavioral responses of the test larvae. Chivers et al. (1997) documented that antipredator responses of larval long-toed salamanders to cues of cannibals included reduced movement and spatially avoiding the area near the cannibal. In this study, test larvae exposed to cannibals or typicals fed conspecifics may have demonstrated similar behavioral responses. These behavioral responses likely conflicted with foraging. In our experiment, all test larvae were fed *ad libitum* every other day. We did not attempt to determine if there were differences in the amount of food eaten by test larvae in the different treatments.

In our experiment, we observed that test animals exhibited a reduction in growth rate and a reduction in the time taken to reach metamorphosis in response to stimulus animals that were fed conspecifics over *Tubifex*. We did not observe any differences in the final mass larvae reached at metamorphosis. Other amphibians, including American toads (*Bufo americanus*), have been shown to metamorphose at a smaller size in response to the nonlethal presence of predators (Skelly and Werner, 1990).

We suggest that the responses exhibited by larvae in this study were mediated by chemical cues. Previously, we found that larval *A. macrodactylum* demonstrated antipredator behavior when exposed to both the chemical and visual cues of the cannibal morphs or chemical cues only, but not when exposed only to visual cues (Chivers et al., 1997). Moreover, the intensity of this antipredator behavior to chemical cues appeared to be elevated when the cannibal morphs were fed a diet of conspecifics (prior to behavioral trials) compared to when the cannibals were fed a diet of *Tubifex*. Therefore, we concluded that larvae were primarily using information from chemical cues to assess their sur-

roundings. Similarly, in the current study, shifts in life-history behavior demonstrated by larvae were likely a response to chemical cues arising as a by-product of the cannibal diet that the stimulus larvae had consumed.

Even though we have no evidence that larval long-toed salamanders use visual or tactile means to recognize predatory cues, we cannot completely rule out this possibility. It is possible that these cues could have been used by larvae in our experiment. The fiberglass mesh screen separating the test larvae from the stimulus larva allowed visual and tactile as well as chemical cues to be exchanged between the test and stimulus larvae. Test larvae could see the stimulus larva in the act of eating and detect any movement associated with this. Visually detecting a stimulus larva consuming a conspecific could have contributed to the shifts in life history observed.

It is not uncommon for adult long-toed salamanders to lay their eggs in temporary environments (Leonard et al., 1993; Wildy, personal observation). Consequently, it is critical for larvae developing in these habitats to metamorphose before the habitat completely dries. In our experiment, we observed that larval salamanders exhibited a reduction in growth rate and an increase in time taken to reach metamorphosis in response to the threat of cannibalism. These responses may be particularly costly in ephemeral environments; the pond may dry prior to the larvae reaching metamorphosis.

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