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SHIFTS IN LIFE HISTORY AS A RESPONSE TO PREDATION IN WESTERN TOADS (*Bufo boreas*)

DOUGLAS P. CHIVERS,[1,*] JOSEPH M. KIESECKER,[2]
ADOLFO MARCO,[3] ERICA L. WILDY,[4]
and ANDREW R. BLAUSTEIN[4]

[1]*Department of Biological Sciences*
University of Maine
Orono, Maine 04469-5751

[2]*School of Forestry and Environmental Studies*
Yale University
New Haven, Connecticut 06511

[3]*Departamento de Biologia Animal*
Universidad de Salamanca
Salamanca, 37071, Spain

[4]*Department of Zoology*
Oregon State University
Corvallis, Oregon 97331

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Abstract—Larval western toads (*Bufo boreas*) are known to exhibit antipredator behavior in response to both chemical alarm cues released from injured conspecifics and chemical cues of predatory invertebrates. In this study, we tested whether long-term exposure to predator and alarm cues resulted in an adaptive shift in life history characteristics of the toads. We raised groups of tadpoles in the presence of: (1) predatory backswimmers (*Notonecta* spp.) that were fed toad tadpoles, (2) nonpredatory water boatman (Corixidae), and (3) chemical alarm cues of injured conspecifics. Tadpoles raised in the presence of both chemical alarm cues and cues of predators fed tadpoles metamorphosed in significantly shorter time than those raised in the presence of the nonpredator control. Reducing time taken to reach metamorphosis would reduce exposure to aquatic predators. There was no difference among treatments in the size at metamorphosis. Our results suggest that this shift in metamorphic characteristics may represent a facultative alteration in life history.

Key Words—Predation, life history, chemical cues, alarm cues, amphibians, western toads, *Bufo boreas*.

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[*] To whom correspondence should be addressed at Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, Saskatchewan S7N 5E2, Canada.

INTRODUCTION

Predation is a strong selective force influencing the behavior, morphology, and life history of prey species (Sih, 1987; Lima and Dill, 1990; Chivers and Smith, 1998). Most studies of prey defenses have concentrated on behavioral or morphological defenses. Fewer studies have examined the effects of predation on alterations in life history characteristics (patterns of growth and reproduction).

Amphibians provide a model system for studying the effects of predation on life history shifts (see Werner, 1986). For example, Skelly (1992) found that gray treefrog (*Hyla versicolor*) tadpoles had reduced growth and development rates when exposed to caged larval tiger salamanders (*Ambystoma tigrinum*). Skelly and Werner (1990) demonstrated that larval American toads (*Bufo americanus*) metamorphosed at a smaller size in the presence of dragonfly (*Anax junius*) predators than in their absence. Van Buskirk (1988) and Wilbur and Fauth (1990) documented that American toad tadpoles metamorphosed earlier and at a smaller size in the presence of dragonfly predators.

Few studies have examined the importance of chemical cues as signals inducing changes in amphibian life history traits (Kats and Dill, 1998). In one study, Sih and Moore (1993) demonstrated that salamanders (*Ambystoma barbouri*) delayed hatching in the presence of chemical cues of predatory flatworms (*Phagocottus gracilis*), but not in response to cues of nonpredatory isopods (*Lirceus fontinalis*). In another study, larval long-toed salamanders (*Ambystoma macrodactylum*) exhibited slower growth and an increase in time to reach metamorphosis in the presence of conspecific predators fed a cannibal diet over conspecifics fed an invertebrate diet (Wildy et al., 1999).

Behavioral responses of larval amphibians to chemical cues are widespread (reviews Chivers and Smith, 1998; Kats and Dill, 1998). For example, several bufonid tadpoles, including those of the western toad, exhibit antipredator behavior to chemical alarm cues released from injured conspecifics (Pfeiffer, 1966; Hews and Blaustein, 1985; Hews, 1988; Petranka, 1989). The specific chemical that acts as the alarm cue for bufonid tadpoles may be bufotoxin (Kulzer, 1954). Bufonid tadpoles also respond to chemical cues of potential predators. For example, Kiesecker et al. (1996) demonstrated that western toad tadpoles exhibit antipredator behavior in response to chemical cues of predatory backswimmers (*Notonecta* spp.), giant waterbugs (*Lethocerus americanus*), and garter snakes (*Thamnophis sirtalis*). Chemical cues are of prime importance in recognition of insect predators by western toad tadpoles. Tadpoles respond to chemical but not visual cues of predatory backswimmers and giant waterbugs (Kiesecker et al., 1996).

In this study, we examined the effects of predation risk on life history characteristics of western toads (*Bufo boreas*). We raised tadpoles in the presence of predatory backswimmers, nonpredatory water boatman, or chemical cues from injured conspecifics to test whether the tadpoles change characteristics of their life history in response to predation cues. Specifically, we tested whether the risk of predation alters the time it takes tadpoles to reach metamorphosis or the size the individuals attain upon reaching metamorphosis.

METHODS AND MATERIALS

We collected larval toad tadpoles from Lost Lake, Linn County, Oregon (44°26′42″N, 121°55′30″W) in the summer of 1996. The tadpoles were transported to Oregon State University for testing. Prior to beginning experiments, tadpoles were maintained in 37-liter glass aquaria on a 14L : 10D photoperiod at approximately 20°C. The tadpoles were fed ad libitum with ground alfalfa pellets.

We divided 12 glass aquaria widthwise with a fiberglass mesh screen to create two compartments, each measuring 25 × 30 × 25 cm. Twelve randomly selected tadpoles were placed onto one side of each of the 12 test tanks. All tadpoles were at the same stage of development (Gosner stage 25) (Gosner, 1960) at the beginning of the experiment. An additional three tadpoles were placed onto the opposite side of each tank from where the test tadpoles were placed. Our experiment consisted of raising groups of tadpoles under three different treatments in a randomized block design with four replicates of each treatment. Treatment 1 was a predator treatment. In this treatment we placed three predatory backswimmers into each aquarium. The predators were placed at the stimulus end of the tank (i.e., the end opposite from where the 12 test tadpoles were housed). Treatment 2 was a nonpredator treatment in which we placed three nonpredatory water boatman into the stimulus end of each aquarium. Treatment 3 consisted of exposing test tadpoles to alarm cues from injured conspecifics.

Throughout the course of the experiment we ensured that there were three live tadpoles on the stimulus end of each aquarium each day. These tadpoles served as prey for the backswimmers. Placement of tadpoles on the stimulus end in the other treatments controlled for any effects related to the presence of prey tadpoles in the backswimmer treatment. We prepared the alarm cue stimulus by grinding a single tadpole with a mortar and pestle in 60 ml of distilled water. The resulting solution was filtered through a fine mesh net and 10 ml of the solution was added to each of the alarm cue treatment containers. Alarm cues were added to the aquaria three days per week. On all occasions the cues were introduced into the stimulus end of the tank.

Throughout the course of the experiment we fed the tadpoles ad libitum with ground alfalfa pellets. The aquaria were cleaned once per week. We monitored the experimental aquaria daily. All test animals that reached metamorphosis (Gosner stage 41) (Gosner, 1960) were removed from the aquaria and weighed.

For each aquarium we calculated the mean time tadpoles took to reach metamorphosis, and the mean mass at metamorphosis. Tank means were used in all statistical analyses. We used a multivariate analysis of variance (MANOVA) to examine the effects of the treatment conditions on metamorphic characteristics of the toads (Tabachnick and Fidell, 1989). After MANOVA, we used univariate analysis of variance (ANOVA) on each of the response variables (time taken to reach metamorphosis, size upon reaching metamorphosis, survival to metamorphosis) to assess which variables were responsible for significant main effects. Post hoc comparisons (Tukey tests) were performed to test for differences between means among the stimuli presented.

RESULTS

MANOVA revealed that there was an overall effect of the treatment conditions on the life history parameters that we measured (Table 1). A subsequent ANOVA showed that time taken to reach metamorphosis was significantly affected by the treatment condition. Tukey tests revealed that tadpoles metamorphosed faster in the presence of alarm cues than in the nonpredator control ($P = 0.029$). Similarly, tadpoles metamorphosed faster in the presence of predator cues than in the presence of nonpredator control cues ($P = 0.025$). There was no difference in time to metamorphosis between the predator and alarm cue treatments ($P > 0.95$). Neither mass at metamorphosis nor survival to metamorphosis was influenced by the treatment conditions (Figure 1). Percentage of survival (mean ± SE) to metamorphosis was 66.7 ± 8.3, 64.5 ± 10.5, and 60.4 ± 8.6 in the predator, nonpredator and alarm cue treatments, respectively.

TABLE 1. RESULTS OF MANOVA FOR OVERALL EFFECTS OF TREATMENT CONDITIONS ON METAMORPHIC TRAITS OF WESTERN TOADS AND ANOVAS FOR EACH RESPONSE VARIABLE[a]

	F	*df*	*P*
MANOVA	14.909	9, 17	<0.001
ANOVA			
Time	6.800	2, 9	0.016
Mass	1.764	2, 9	0.226
Survival	0.121	2, 9	0.888

[a] Response variables are time to reach metamorphosis (time), mass at metamorphosis (mass), and survival to metamorphosis (survival).

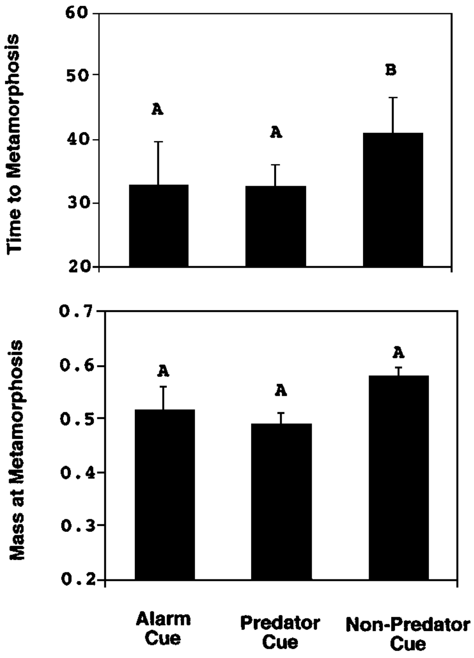

FIG. 1. Mean (+ SE) time to reach metamorphosis (days) and mean mass at metamorphosis (grams) for tadpoles exposed to chemical cues of injured conspecifics, cues of predatory backswimmers, and cues of nonpredatory water boatman. Different letters denote significant differences at $P < 0.05$, based on post-hoc Tukey tests.

DISCUSSION

The results of our study demonstrate that western toads alter characteristics of their life history in response to cues that indicate predation. Tadpoles decrease time taken to reach metamorphosis in the presence of predator cues and alarm cues when compared to nonpredator cues. By decreasing time taken to reach metamorphosis, toads likely benefit by reducing the time they are exposed to predation by aquatic predators. Nevertheless, this type of shift in life history may have potential costs. For example, early metamorphosis may expose toads to a higher level of terrestrial predation. Further experiments are needed to understand potential costs of early metamorphosis.

Kiesecker et al. (1996) showed that western toad tadpoles do not respond to visual cues of invertebrate predators (backswimmers and giant waterbugs), but do respond to chemical cues of the same predators. In this experiment we fed the backswimmers tadpoles in the experimental aquaria. Consequently, our predator stimulus likely resulted in a complex stimulus that included both visual and chemical cues of the predator and injured prey cues. We know that both this complex predator stimulus and the injured prey (alarm) cues alone will induce the change in life history. It is important to stress that we do not know whether cues from the predator in the absence of alarm cues (bufotoxin) of the prey will induce this change in life history. The response to the predator stimulus that we observed may be a direct response to the alarm cues of injured prey and not a response to the predator per se.

Additional studies designed at examining the nature of the chemically induced life history changes are warranted. For example, future studies should manipulate the concentration and frequency of exposure to alarm cues in order to assess whether the change in life history is an all-or-nothing response or instead is a graded response that reflects the intensity of predation. Moreover, we should more closely examine the nature of the chemical cues that induce the changes, not only the chemistry of the stimulus but also its perception and the mechanism of response by the tadpoles. We know that alarm cues alone will induce a shift in life history. The response to the predator stimulus in our study may have been a response to the predator stimulus alone, it may have been a response to alarm cues released when the predator captured the prey, or alternatively it may be a response to alarm cues released in the predator's diet. Several behavioral studies indicate that prey species may only respond to chemical cues of a predator when the predator is fed a diet that contains conspecifics of the prey (e.g., Mathis and Smith, 1993; Wilson and Lefcort, 1993; Chivers et al., 1996). Similar results are known in studies of morphological defenses. For example, Stabell and Lwin (1997) showed that crucian carp (*Carassius carassius*) exhibit an adaptive change in body morphology in response to predators fed carp but not predators fed a different diet.

In our experiment the response of the toads was to decrease the time taken to reach metamorphosis. We found no evidence that tadpoles metamorphosed at a different size in the presence of the predator or alarm cues than in the presence of nonpredator cues. Van Buskirk (1988) and Wilbur and Fauth (1990) showed that American toad tadpoles decreased both the time taken to reach metamorphosis and the size at metamorphosis in response to dragonfly predators. In another study, Skelly and Werner (1990) found that American toads metamorphosed at a smaller size in the presence of larval dragonflies. They found no evidence that toad tadpoles reduced the time taken to reach metamorphosis.

Long-term shifts in life history may result from several factors. For example, numerous authors (e.g., Dodson and Havel, 1988; Skelly, 1992; Ball and Baker, 1996) have demonstrated that life history shifts may result as by-products of antipredator behavior. Specifically, time and energy devoted to antipredator responses have a cost in terms of a reduction in growth and/or development rate. Such reductions in growth and/or development rate could influence the timing of life history switch points, for example, by either decreasing size at metamorphosis or increasing time to metamorphosis or both. Long-term shifts in life history may also represent facultative alterations in development rate, whereby animals increase their development rate while maintaining the same growth rate (e.g., Minchella and Loverde, 1981; Crowl and Covich, 1990; Wilbur and Fauth, 1990). This type of change would likely decrease the time taken to reach metamorphosis.

Changes in timing of metamorphosis or size at metamorphosis can occur even in the absence of a facultative increase in development rate or a decrease in growth and/or development rate associated with antipredator behavior. For example, if tadpoles have reached a plateau on their growth curve and if the conditions in the terrestrial environment are harsh or unpredictable, then in the absence of aquatic predators, tadpoles may not transform even in an aquatic environment that provides little or no growth opportunities. If this was the case, the costs of staying in the aquatic environment and not growing must outweigh costs in the terrestrial environment. It may be common to have temporary periods during which growth and/or survival is lower in the terrestrial environment than the aquatic environment. Such conditions could occur, for example, if the probability of desiccation is high or if terrestrial predators are concentrated at the edge of the water (DeVito et al., 1998).

In our experiment we documented that tadpoles were the same size at metamorphosis, but metamorphosed faster in the presence of the alarm and predator cues than in the presence of the nonpredator cues. We do not know whether tadpoles in the different treatments exhibited the same growth and/or development rate throughout the experiment. It is possible that differences in the timing of metamorphosis that we observed could result from a facultative increase in development rate. Alternatively, the tadpoles may have had the same growth and development rate but altered their timing of metamorphosis to reflect differences in costs and benefits of transforming. Future studies are needed to differentiate these possibilities.

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