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Predator-induced life history changes in amphibians: egg predation induces hatching

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The timing of transitions between life history stages should be affected by factors that influence survival and growth of organisms in adjacent life history stages. In a series of laboratory experiments, we examined the influence of predation risk as a cue to trigger a life history switch in amphibians. In the Oregon Cascade Mountains, some populations of Pacific treefrogs (*Hyla regilla*) and Cascades frogs (*Rana cascadae*) are under intense egg predation by predatory leeches (families Glossiphonidae and Erpobdellidae). We document that both treefrogs and Cascades frogs show plasticity in hatching characteristics in response to the threat of egg predation. Pacific treefrogs hatch sooner and at an earlier developmental stage when either predatory leeches or non-predatory earthworms are allowed direct contact with the developing egg mass. The same response is elicited even without direct contact. Chemical cues of predatory leeches and chemicals released from injured eggs appear to elicit the same early hatching response in treefrogs. For Cascades frogs, cues of leeches, but not those of injured eggs, elicit an early hatching response. Hatching early in response to egg predators may reduce predation. Plasticity of hatching characteristics has rarely been examined. However, we suspect that it may be common, particularly in populations or species that experience high variability in predation pressure between years.

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Predation has long been recognized as a strong selective force that influences the behavior, morphology and life history of prey species (Reviews: Havel 1987, Sih 1987, Lima and Dill 1990, Chivers and Smith 1998). Studies of the effects of predation on prey responses are biased towards studies of behavior and morphology. Nevertheless, exposure to predators have been shown to influence prey life history switch points, including those related to the timing of hatching (e.g. Sih and Moore 1993, Warkentin 1995), metamorphosis (e.g. Werner 1986, Skelly and Werner 1990, Rowe and Ludwig 1991, Skelly 1992, DeVito et al. 1998) and reproduction (e.g. Mangel and Clark 1988, Crowl and Covich 1990, Reznick et al. 1990, Ball and Baker 1996). The timing of life history switch points will be affected by factors that influence survival and rates of growth and development of the organism in adjacent life history stages (Werner 1986, Rowe and Ludwig 1991). Specifically, organisms should switch life history stages when their mortality/

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growth ratio is lower in the following stage than the current stage.

Empirical studies of predator-induced changes in hatching characteristics are rare. This is surprising if one considers that embryos are a major prey item for many predators, yet embryos have limited options for mediating predation risk. In one study, Livdahl et al. (1984) showed that mosquitoes (*Aedes triseriatus*) reduced hatching when conspecific larvae were present in the water. Reduced hatching may be a response to avoid competition and/or predation on hatchlings, since conspecifics are both potential competitors and predators. In another study, Blaustein (1997) showed that crustaceans (*Arctodiaptomus similis*, *Ceriodaphnia quadrangulu*, *Cyzicus* sp.) were less abundant in the presence of salamanders (*Salamandra infraimmaculata*) than in their absence, and hypothesized that the difference in abundance was likely due to hatching inhibition.

Amphibians provide a model system for studying the effects of predation on life history shifts (e.g. Werner 1986). However, the amphibian system has been examined almost exclusively from the perspective of predation effects on metamorphosis. Two recent studies have demonstrated that amphibians may also exhibit adaptive plasticity in hatching characteristics. Sih and Moore (1993) incubated salamander eggs (*Ambystoma barbouri*) in direct contact with flatworms (*Phagocottus gracilis*) and isopods (*Lirceus fontinalis*). Flatworms are potential predators on hatchling salamander larvae but isopods are not. The salamanders delayed hatching in response to flatworms but not in response to isopods (Sih and Moore 1993). By delaying hatching, salamanders reach a developmental stage where they are less susceptible to predation by flatworms. In another study, Warkentin (1995) showed that arboreal eggs of the red-eyed tree frog (*Agalychnis callidryas*) hatch faster when the eggs are attacked by snake predators than when left undisturbed. By hatching, the tadpoles escape predation by falling into the water below the nest.

It is unknown whether adaptive plasticity in hatching characteristics is widespread in predator/prey systems. In this study, we examined the effects of predation risk on hatching characteristics of two species of anurans, the Pacific tree frog (*Hyla regilla*) and the Cascades frog (*Rana cascadae*). At sites in the Cascade Mountains of central Oregon, eggs of both of these species are vulnerable to predation by leeches in the families Glossiphoniidae and Erpobdellidae. In this study, we used a series of laboratory experiments to test whether predation on eggs influenced the hatching characteristics of either species, and the proximate cues used to induce the changes.

Experiment 1: Hatching responses of Pacific treefrogs to live leech predators

Methods

The purpose of this experiment was to test whether the presence of a potential egg predator influences the hatching characteristics of *H. regilla*. In April 1996, we collected *H. regilla* clutches from a montane pond located 89 km east of Albany, Linn County, Oregon, where they co-occur with predatory leeches. The eggs were transported to Oregon State University for testing.

In the laboratory we identified seven clutches of eggs that had reached Gosner stage 19 or 20 (Gosner 1960) for use in the experiment. We carefully separated each of the seven clutches into three approximately equal sized masses, and then placed each of the 21 masses into an individual 0.7-L round plastic container (10 cm diameter) filled with dechlorinated tap water. We randomly assigned the three egg masses from each of the original seven clutches to one of three treatment conditions: (1) a control treatment where nothing was added to containers with the eggs, (2) a predator treatment where a single leech (*Desserobdella picta*, mean $\pm$ 1 SD = 0.59 $\pm$ 0.20 g) was added to the container with the eggs, and (3) a non-predator treatment where a single earthworm (*Lumbricus terrestris*, mean $\pm$ 1 SD = 5.47 $\pm$ 1.35 g) was added to the container with the eggs. There was a mean of 22.1 $\pm$ 8.3, 19.3 $\pm$ 5.0 and 14.9 $\pm$ 2.8 eggs in the predator, non-predator and control treatments, respectively. ANOVA showed that there was no significant difference in the initial number of eggs between the three treatments ($F_{2,18} = 2.78$, $P > 0.05$).

The experiment was conducted on a 14:10 L:D photoperiod at approximately 20°C. At 6-h intervals throughout the experiment we monitored the containers for the presence of tadpoles. At each 6-h monitoring period we used a pipette to remove all tadpoles that hatched in the preceding 6-h period. The experiment ended after all eggs had either hatched or died. A single experimenter, who was blind to the treatment conditions, determined the developmental stage of the newly hatched tadpoles (according to Gosner 1960) and measured the total length of each tadpole to the nearest 0.1 mm.

For each container we calculated the average time, size and developmental stage at which the tadpoles hatched, and used a multivariate analysis of variance (MANOVA) to test for treatment effects (Tabachnick and Fidell 1989). Our assessment of tadpole size was based on length not volume. This means that a tadpole that was smaller in length was not necessarily smaller in volume. After the MANOVA we used univariate analysis of variance (ANOVA) on each response variable to assess which variables were responsible for significant main effects. This was followed by post hoc compari-

sons (Tukey tests) to test for significant differences between treatment means.

Results

The percentage of eggs that hatched was high in all three treatments (mean $\pm$ SD = 95.3 $\pm$ 7.1, 96.9 $\pm$ 6.8 and 91.5 $\pm$ 8.0 for the control, predator and non-predator treatments, respectively). A MANOVA revealed that the treatment condition had a significant effect on the hatching characteristics of *H. regilla* (Table 1). Subsequent ANOVAs showed that time to hatching and developmental stage at hatching, but not size at hatching was significantly affected by treatment condition (Table 1). Tadpoles hatched earlier and at a less developed stage in the predator (leech) and non-predator (earthworm) treatment than in the control treatment ($P < 0.005$ for all comparisons, Fig. 1). The lack of a significant difference in size at hatching may be a consequence of the naturally large variability in hatching size. In six of seven replicates, the mean sizes of hatching tadpoles in the control treatment were larger than those in either the predator or non-predator treatments. There was no significant difference in either time to or stage at hatching between the predator and non-predator treatments ($P > 0.90$ for both comparisons, Fig. 1).

Table 1. Results of MANOVA for overall effects of treatment types on hatching characteristics and ANOVAs for each response variable. For experiments 1 and 2 response variables are mean time to hatch (time), mean size at hatching (size), and mean developmental stage at hatching (stage). For experiment 3, response variables are mean time to hatch (time), mean time to leave jelly mass after hatching (leave), mean size upon leaving jelly mass (size) and mean developmental stage upon leaving jelly mass (stage).

	F	d.f.	*P*
Experiment 1. Hatching responses of Pacific treefrogs to live predators			
MANOVA	5.479	6, 32	0.001
ANOVAs			
Time	13.731	2, 18	<0.001
Size	1.452	2, 18	0.260
Stage	21.023	2, 18	<0.001
Experiment 2. Hatching responses of Pacific tree frogs to non contact preditor cues			
MANOVA	6.153	9, 82	<0.001
ANOVAs			
Time	5.177	3, 36	0.004
Size	6.219	3, 36	0.002
Stage	22.661	3, 36	<0.001
Experiment 3. Hatching responses of Cascades frogs to non-contact predator cues			
MANOVA	14.175	16, 101	<0.001
ANOVAs			
Time	4.686	3, 36	0.007
Size	37.015	3, 36	<0.001
Stage	12.261	3, 36	<0.001
Leave	60.481	3, 36	<0.001

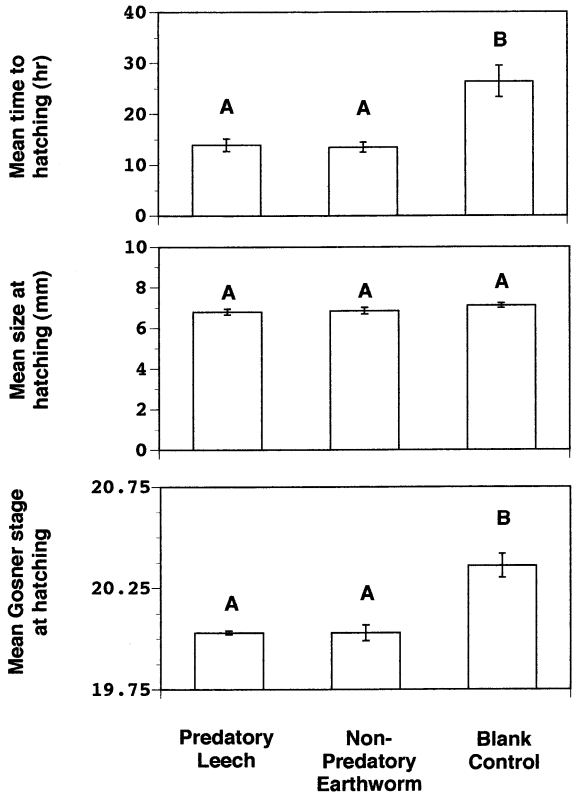

Fig. 1. Mean ($\pm$SE) time, size and developmental stage at hatching for Pacific treefrogs exposed to direct contact with cues of predatory leeches, non-predator earthworms or nothing (blank control). Different letters over bars indicate significant differences at $P < 0.05$, based on Tukey tests).

Experiment 2: Hatching responses of Pacific treefrogs to non-contact predator cues

Methods

The purpose of this experiment was to test whether *H. regilla* alter their hatching characteristics in response to non-contact cues that indicate predation risk. Eggs were tested under four treatment conditions: (1) predator, (2) non-predator, (3) injured egg, and (4) distilled water control. The eggs used in this study were collected from the same location as the eggs in the previous experiment.

We placed four randomly selected intact clutches of eggs into each of 40 rectangular plastic containers (45 $\times$ 24 $\times$ 15 cm) that were filled to a depth of 12 cm with dechlorinated tap water. These clutches represent the test eggs that we monitored throughout the experiment. This density of eggs is within that observed under natural conditions (Kiesecker and Blaustein 1997). There were no significant differences in either the number ($F_{3,36} = 0.476$, $P = 0.701$) or developmental stage ($F_{3,36} = 0.223$, $P = 0.880$) of the eggs among the four treatments at the beginning of the experiment (Table 2).

In the center of each of the 40 containers we also placed a mesh enclosure ($10 \times 10 \times 7.5$ cm) that contained 50 *H. regilla* eggs. We added five leeches (mean $\pm$ SD mass $= 0.74 \pm 0.27$ g) to the central mesh enclosure of each of the predator treatment containers. Eggs in the central enclosures were used simply to provide food for the leeches throughout the experiment. Hatching characteristics of these eggs were not monitored. In the non-predator treatment we added two earthworms (mean $\pm$ SD mass $= 5.41 \pm 1.15$ g) to the central enclosure. In the control and injured egg treatments nothing was added to the inside of the mesh enclosures with the 50 eggs. However, at 06.00 and 18.00 each day of the experiment we slowly added 5 mL of injured egg solution to the center of each injured egg treatment container. To prepare the injured egg solution we ground 30 *H. regilla* eggs with a mortar and pestle and added distilled water to bring the solution to 50 mL. The injured egg solution was used within minutes of preparation. Each 5 mL of injured egg solution contained the equivalent of three injured eggs; therefore, we added the equivalent of six injured eggs to each injured egg container per day. At the same time we introduced the injured egg solution we added 5 mL of distilled water to the center of each of the 10 control containers. This controlled for any effects related to the disturbance of introducing the injured egg solution. The experiment was conducted on a 14:10 L:D photoperiod at approximately 20°C.

Throughout the course of the experiment we removed each of the central mesh enclosures every other day and replaced any missing or dead eggs. This ensured that a continual supply of eggs was available to the leeches throughout the experiment. There was a mean ($\pm$ SD) of 5.34 ± 1.20 eggs per day missing from the central mesh enclosures in the predator treatment. We are unsure of the exact number of eggs eaten by the leeches, as some eggs could have died and disintegrated over the interval between monitoring the enclosures for missing eggs. However, this level of missing eggs compares to a mean ($\pm$ SD) of 0.82 ± 0.28, 0.63 ± 0.28 and 0.54 ± 0.15 eggs per day missing from the central enclosures in the non-predator, injured egg and control treatments, respectively. The average number of eggs missing from the predator treatment (5.4 eggs per day) is comparable to the number of eggs we used in the injured egg treatment (six eggs per day).

Table 2. Mean ($\pm$ SE) number and developmental stage of eggs in each of the four treatments at the start of experiment 2. There was no difference between treatments in either the number of eggs or developmental stage of eggs between treatments (see text for details).

Treatment	Number of eggs	Stage of eggs
Predator (leech)	152.9 ± 9.9	14.5 ± 0.3
Non-predator (earthworm)	153.2 ± 7.5	14.1 ± 0.5
Injured egg	162.8 ± 7.2	14.1 ± 0.4
Control	150.4 ± 6.8	14.3 ± 0.6

As in experiment 1, we monitored the containers every 6 h for tadpoles. At each monitoring period we used a pipette to remove all test tadpoles that hatched in the preceding 6-h period. The experiment ended when all eggs either hatched or died. A single experimenter, who was blind to the treatment conditions, determined the developmental stage (according to Gosner 1960) and measured the total length of each tadpole to the nearest 0.1 mm. We calculated the average time, size and developmental stage at which the tadpoles hatched in each container and assessed differences in hatching characteristics among the treatments using the same statistical approach as in experiment 1.

Results

Percent survival of test animals to hatching was relatively high (mean $\pm$ SD $= 88.2 \pm 10.8$, 90.3 ± 10.6, 93.8 ± 7.7 and 87.3 ± 15.5 for the predator, non-predator, injured egg and control treatments respectively). This survival rate is comparable to that observed under natural conditions (e.g. Kiesecker and Blaustein 1997).

A MANOVA revealed that the treatment condition had a significant effect on the hatching characteristics of *H. regilla* (Table 1). Subsequent ANOVAs showed that time, size and developmental stage at hatching were significantly affected by the treatment condition. Tadpoles hatched in less time, at a smaller size and earlier developmental stage in the predator treatment compared to the non-predator treatment or distilled water control treatment ($P < 0.05$ for all comparisons, Fig. 2). However, there was no difference between the predator treatment and the injured egg treatment ($P > 0.50$ for all comparisons, Fig. 2). Tadpoles in the injured egg treatment hatched at a smaller size and earlier developmental stage than those in the control treatment ($P < 0.05$, Fig. 2). There was also a strong trend for tadpoles in the injured egg treatment to hatch earlier than those in the control treatment ($P = 0.052$, Fig. 2). Tadpoles in the injured egg treatment hatched at an earlier developmental stage than those in the non-predator treatment. Time to and size at hatching was not significantly different between the injured egg treatment and the non-predator treatment; however, trends were evident ($P = 0.095$ and 0.057 for time and size, respectively). Neither time, size nor developmental stage at hatching differed between the control and non-predator treatments ($P > 0.30$ for all comparisons, Fig. 2).

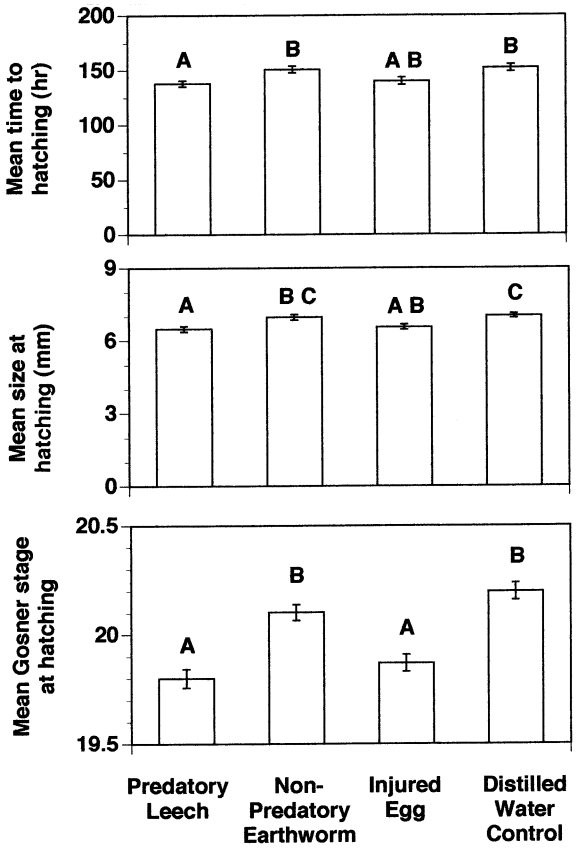

Fig. 2. Mean ($\pm$SE) time, size and developmental stage at hatching for Pacific treefrogs exposed to non-contact cues of predatory leeches, non-predatory earthworms, injured eggs or a distilled water control. Different letters over bars indicate significant differences at $P < 0.05$, based on Tukey tests).

Experiment 3: Hatching responses of Cascades frogs to non-contact predator cues

Methods

The purpose of this experiment was to test whether *R. cascadae* alter their hatching characteristics in response to non-contact cues that indicate predation risk. We collected *R. cascadae* eggs from the same location as we collected *H. regilla* eggs for the previous experiments. The design of this experiment was similar to that of experiment 2. However, in this experiment we placed only 25 eggs (five eggs from each of five clutches, mean $\pm$ SD Gosner stage $= 16.8 \pm 1.5$) into each of the 40 rectangular testing containers. Also, in the central mesh enclosures in each of the containers we added only 10 *R. cascadae* eggs. Furthermore, we prepared the injured egg solution by grinding only 13 eggs. Each 5 mL of injured egg solution contained the equivalent of 1.3 injured eggs; consequently, we added the equivalent of 2.6 injured eggs to each injured egg treatment container per day.

There was a mean ($\pm$SD) of 4.27 ± 0.75, 0.34 ± 0.22, 0.34 ± 0.13, and 0.32 ± 0.19 eggs per day missing from central mesh enclosures of the predator, non-predator, injured egg and control treatment containers, respectively. The average of 4.27 eggs per day missing from the predator treatment containers was somewhat greater than the 2.60 injured eggs we introduced to the injured egg treatment containers each day.

In this experiment, we collected data on a different set of response variables than experiments 1 and 2. Unlike *H. regilla* tadpoles that leave the egg mass immediately upon hatching, *R. cascadae* tadpoles remain attached to the jelly mass for several hours or days before swimming away (Nussbaum et al. 1983, Kiesecker unpubl.). Therefore, we quantified both time to hatching and time to leave the jelly mass after hatching. We considered the eggs hatched when the vitelline membrane was ruptured, which was easily observed because the tadpoles straightened from their previously curved position within the egg. We considered the tadpole to have left the jelly mass when they no longer made contact with it. We also quantified the size and developmental stage of the tadpoles upon leaving the jelly mass. We used the same statistical approach as the other experiments, except that we had four response variables in our MANOVA model.

Results

Mean ($\pm$SD) survival of test animals to hatching was 96.0 ± 5.0, 97.6 ± 3.9, 97.2 ± 2.7, 98.0 ± 3.9 for the predator, non-predator, injured egg and control treatments, respectively. A MANOVA revealed that the treatment condition had a significant effect on the hatching characteristics of *R. cascadae* (Table 1). Subsequent ANOVAs showed that time to hatching, time to leave jelly mass after hatching, and size and developmental stage upon leaving the jelly mass were all significantly affected by the treatment condition (Fig. 3). Tadpoles hatched in less time, left the egg mass sooner after hatching, and were a smaller size and earlier developmental stage upon leaving the jelly mass in the predator treatment compared to the non-predator treatment or distilled water control treatment ($P < 0.05$ for all comparisons, Fig. 3) but not the injured egg treatment ($P > 0.15$ for all comparisons, Fig. 3). Tadpoles in the injured egg treatment left the egg mass sooner after hatching and were a smaller size and earlier developmental stage upon leaving the egg mass than those in the non-predator and control treatments ($P < 0.05$ for all comparisons, Fig. 3). However, tadpoles in the injured egg treatments did not hatch faster than those in either the non-predator or control treatments ($P > 0.40$ for both comparisons, Fig. 3). Neither time to hatching, time to leave the jelly mass after hatching nor size or developmental stage upon leaving the jelly mass

differed between the control and non-predator treatments ($P > 0.80$ for all comparisons, Fig. 3).

Discussion

Our study suggests that both Pacific treefrogs and Cascades frogs show considerable plasticity in their hatching characteristics. By hatching early in response to egg predators, these amphibians may reduce their likelihood of being eaten.

In experiment 1, Pacific treefrogs hatched earlier and at a less developed stage when in direct contact with leech predators than in the control treatment. The same pattern was observed in the non-predator treatment; eggs hatched earlier and at a less developed stage in response to direct contact with the non-predatory earthworms than in the control treatment. These results suggest that direct mechanical contact between the egg mass and a potential predator may induce earlier hatching. Warkentin (1995) showed that red-eyed treefrogs hatched earlier in response to direct contact with cat-eyed snakes. In her study, touching and moving the eggs simultaneously by sliding forceps between the egg and jelly mass was effective at inducing early hatching. However, neither touching the eggs nor moving the eggs by pulling the jelly were effective alone as cues to induce early hatching (Warkentin 1995). Additional studies are needed to determine how much contact is needed in order to induce earlier hatching in Pacific treefrogs.

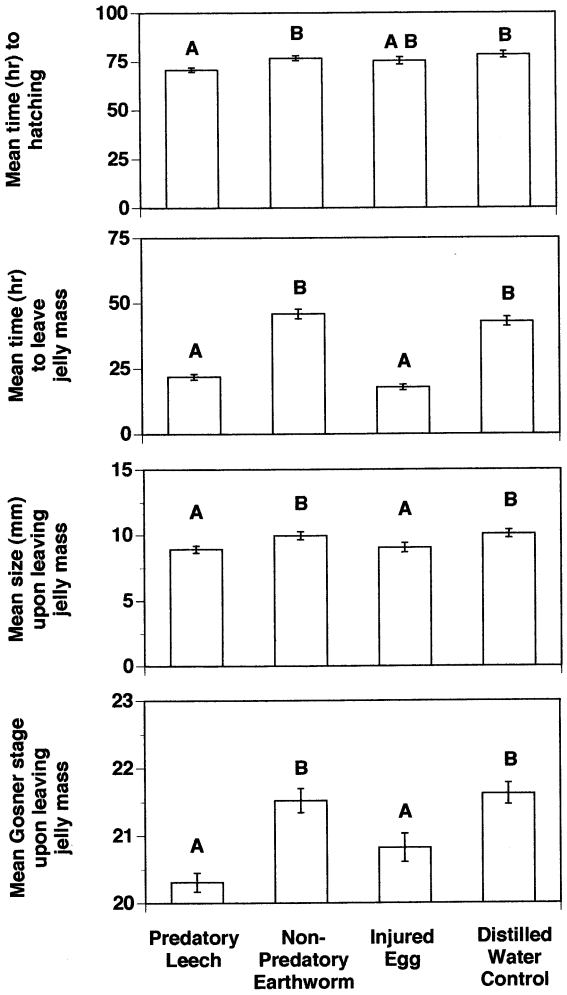

Fig. 3. Mean ($\pm$ SE) time to hatching and mean time, size and developmental stage to leave jelly mass after hatching for Cascades frogs exposed to non-contact cues of predatory leeches, non-predatory earthworms, injured eggs or a distilled water control. Different letters over bars indicate significant differences at $P < 0.05$, based on Tukey tests).

Direct contact between a potential predator and an egg mass is not required to induce early hatching in Pacific treefrogs or Cascades frogs. We documented that eggs of both species hatched faster in response to non-contact cues of leeches compared to non-contact cues of earthworms or the distilled water control. We suggest that chemical cues probably triggered the hatching response in the leech treatment, because it is unlikely that mechanical cues could be transmitted through the mesh screen to the eggs. The importance of chemical cues was also demonstrated by the injured egg treatment. For example, Pacific treefrogs were smaller, less developed and tended to hatch earlier in response to a solution of injured eggs than in response to either the distilled water control or the non-predator control. Sih and Moore (1993) also documented that the delayed hatching response of salamander eggs is mediated through chemical cues.

The fact that amphibians may alter hatching characteristics in the absence of direct contact with a predator is important. Prey that can detect and respond to the predator without direct contact may have an advantage over those that need direct contact from predators. The benefits of detecting a nearby predator should be enhanced if the predator is detected earlier rather than later (Lima and Dill 1990). Early warning may afford the prey more options on the most appropriate way to respond to the predator.

Given that no direct contact is required to induce hatching in these systems, a single predator or small number of predators may impact a large number of prey animals. This result may have implications for modeling the dynamics of predator-prey interactions. Many models assume intensity of anti-predator responses are directly related to predation rate. Our results imply that indirect measures of predation risk may be equally important as predation rate.

Recent advances in the field of chemical ecology indicate that prey species often respond differentially to cues of a predator fed different diets (review, Chivers and Smith 1998). For example, several behavioral studies indicate that the anti-predator response is reduced

or absent if the predator is fed a diet that does not contain the prey (e.g. Mathis and Smith 1993, Wilson and Lefcort 1993, Chivers et al. 1996). Stabell and Lwin (1997) recently documented a similar result in a morphological study. They found that crucian carp (*Carassius carassius*) exhibit an adaptive change in body morphology in response to predators fed carp but not predators fed a different fish diet (arctic char, *Salvelinus alpinus*). In our experiment, the leeches in the predator treatment were fed amphibian eggs in the experimental containers. Consequently, our predator stimulus was likely a complex stimulus that included both cues of the predator and injured egg cues. For Pacific treefrogs we have a good indication that cues from injured eggs alone may induce early hatching. It remains unknown whether cues of the leeches in the absence of injured egg cues will induce the change in hatching. In our experiment, Cascades frogs did not hatch sooner in the presence of only chemical cues of injured eggs. However, they did hatch faster in the presence of leeches feeding on eggs. Our experimental design did not allow us to determine whether cues of leeches alone in the absence of cues of injured eggs causes the change in hatching characteristics.

Cascades frog eggs hatched sooner in the predatory leech treatment than in either the non-predatory control or the distilled water control treatments. Cascades frogs did not, however, hatch sooner in response to the injured eggs. This finding differs somewhat from the results of the experiment with Pacific treefrogs. In that experiment, eggs showed a strong trend to hatch sooner in response to both injured eggs and predatory leeches. We caution that this apparent difference between species should be carefully scrutinized. It seems premature to conclude that Cascades frogs do not hatch sooner in response to cues of injured eggs. Cues of injured eggs may induce a change in hatching time if the concentration of cues exceeds a certain threshold. We added the equivalent of 2.6 injured *Rana cascadae* eggs to each injured egg containers each day. This compares to six injured eggs per day added to each container in the treefrog experiment. We should expect a change in hatching characteristics to occur only if the concentration exceeds a certain threshold or if the cues are experienced frequently enough. We suggest that future studies should manipulate the concentration and frequency of exposure to chemical cues of predators. This will allow us to assess whether changes in hatching is an all or nothing response or instead is a graded response that may reflect the intensity of egg predation.

Studies of how vertebrates alter hatching characteristics in response to differences in predation risk are at an early stage. We know of examples of how predation on eggs induces hatching (Warkentin 1995; this study) and ways in which predation on larvae delays hatching (Sih and Moore 1993). We suggest that future studies should examine whether both early and delayed hatching occurs in the same system depending on the intensity of predation by egg versus larval predators. In addition, future studies should attempt to assess if plasticity in hatching is restricted to species or populations with specific predation characteristics. Clark and Harvell (1992) suggested that predator-induced morphological defenses should occur in unpredictable environments where predator attacks are intermittent across generations, whereas fixed defenses should be favored under conditions of high environmental predictability when predators are permanently present. We suggest that the same logic should apply to predator-induced changes in hatching characteristics. Accordingly, we may expect greater plasticity in species or populations with high variability in predation between years. This possibility deserves further exploration.

Throughout the time we completed our research we continually maintained large numbers of leeches in our laboratory. During this time we found no indication that leeches fed on tadpoles. In this type of system it is easy to speculate on the benefits of early hatching. The animals may experience a significantly reduced probability of capture by egg predators. However, there may be substantial costs associated with these early hatching responses. We can speculate that the tadpoles in our study that hatched early would have reduced mobility and reduced sensory abilities. Between Gosner stages 19 and 22 there is increased gill and tail fin circulation as well as substantial changes related to the transparency of the cornea. Reduced mobility and reduced sensory abilities could lead to an increase in vulnerability to tadpole predators. Warkentin (1995) showed that red-eyed treefrogs that hatched earlier in response to snake predators were more vulnerable to both shrimp (*Macrobranchium americanum*) and fish (*Brachyraphis rhabdophora*) predators. There are likely other costs to early hatching responses besides increasing vulnerability to aquatic predators.

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