

AN ABSTRACT OF THE THESIS OF

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Many organisms with complex life cycles undergo transition periods associated with increased vulnerability to predation. Several evolutionary adaptations have been proposed as antipredator defenses for organisms during risky transition periods. These include: shortening of the transition period, parental care, cryptic coloration, and synchrony of risky transitions with large numbers of conspecifics. The results of my research support the hypothesis that synchrony of metamorphosis and emergence from the water and aggregation during the period of transformation may be antipredator defenses for the western toad (*Bufo boreas*). For some anuran species, synchronous metamorphosis may function as an antipredator adaptation by swamping predators during the period of transformation. I examined the levels of synchrony of emergence from the water of metamorphosing western toads (*Bufo boreas*) in the presence and absence of a live snake predator, the common garter snake (*Thamnophis sirtalis*) in a laboratory experiment. To compare between the treatments, I measured the time to emergence from the water, the number of metamorphs emerging together, and the level of aggregation (before and during emergence) of the toads in each treatment. There was a difference between the treatments when all three factors were considered. I attributed these

differences to a behavioral response in which *B. boreas* emerged sooner in the presence of the predator, regardless of whether individual toads had reached the point at which they were physically better suited to the terrestrial environment than the larval environment.

Since the Pacific treefrog (*Hyla regilla*) is also preyed upon by *T. sirtalis* during the vulnerable period of metamorphosis, I conducted a laboratory experiment to test the effects of the presence of *T. sirtalis* on 1) aggregation of larval and metamorphosing *H. regilla*, 2) time to metamorphosis, 3) synchrony of metamorphosis, 4) time to emergence from the water and 5) synchrony of emergence from the water. The only significant effect observed in this experiment was a difference between aggregation levels of *H. regilla* throughout the experiment. There was, however, a strong trend in which the variances around the mean times to metamorphosis and emergence of the frogs in the control treatments were larger than those in the predator treatments. This could indicate a trend toward synchrony of metamorphosis and emergence for *H. regilla* in the presence of snake predators.

THE EFFECTS OF PREDATION ON ANURAN METAMORPHOSIS

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CONTRIBUTION OF AUTHORS

Andrew Blaustein, Douglas Chivers, Joseph Kiesecker, Adolfo Marco, and Erica Wildy were involved in the design and participated in the collection and analysis of data for the experiment presented in chapter II. Andrew Blaustein, Douglas Chivers, Joseph Kiesecker, and Lisa Belden were involved in the design and participated in the collection and analysis of data for the experiment presented in chapter III. My co-authors also provided constructive comments on earlier versions of each manuscript. Both experiments were conducted in the laboratory of Andrew Blaustein.

TABLE OF CONTENTS

	Page
I. GENERAL INTRODUCTION	1
Aggregation as Antipredator Defense	1
Synchrony of Vulnerable Transitions	4
Vulnerability of Anuran Metamorphosis	5
Synchrony and Aggregation as Plastic Responses to Predation	6
II. EFFECTS OF SNAKE PREDATION ON METAMORPHOSIS OF WESTERN TOADS, <i>BUFO BOREAS</i>	8
Introduction	8
Methods	10
Results	13
Discussion	16
III. EFFECTS OF SNAKE PREDATION ON AGGREGATION AND METAMORPHOSIS OF PACIFIC TREEFROG (<i>HYLA REGILLA</i>) LARVAE	21
Introduction	21
Methods	23
Results	25
Discussion	27
IV. GENERAL DISCUSSION	30
BIBLIOGRAPHY	37

LIST OF FIGURES

Figure

1. Mean (\pm SE) time to emergence from the water, mean (\pm SE) level of aggregation, and mean (\pm SE) level of synchrony for *Bufo boreas*. 15
2. Mean (\pm SE) level of aggregation for *Hyla regilla* tadpoles. 26
3. Mean (\pm SE) time to metamorphosis and mean (\pm SE) time to emergence from the water for *H. regilla*. 27

LIST OF TABLES

Table	Page
1. Results of MANOVA for overall effects of <i>Thamnophis sirtalis</i> on time to emergence from the water, and levels of aggregation and synchrony of transforming <i>Bufo boreas</i> .	14
2. Results of equality of variance test for mean time to metamorphosis and mean time to emergence from the water of <i>Hyla regilla</i> larvae.	26

THE EFFECTS OF PREDATION ON ANURAN METAMORPHOSIS

I. GENERAL INTRODUCTION

AGGREGATION AS ANTIPREDATOR DEFENSE

Animals form groups for many reasons. In some cases, group living is a byproduct of the fact that many conspecifics must share an unequally distributed resource (e.g., nesting sites; Alexander 1974). Other reasons for aggregation include: group hunting strategy, location of mates, efficiency of foraging, and antipredator defense (Ward and Zahavi 1973, Alexander 1974, Bertram 1978, Krebs and Inman 1992).

Predation pressure may play a role in the selection for sociality in many prey animals (Crook 1965, Hobson 1978, Pulliam and Caraco 1984, Godin 1986, Pitcher 1986). Membership in a conspecific group can benefit an individual prey animal by increasing its ability to forage efficiently and/or by reducing its chances of predation (Alexander 1974, Bertram in Krebs and Davies 1978 text, Lima and Dill 1990). Animals which form kin groups can also benefit from inclusive fitness (Blaustein et al. 1987).

Prey animals in groups may benefit from increased vigilance and a consequent increase in the efficiency of foraging and other activities. For some social prey animals, the amount of time each individual spends engaged in vigilant behavior decreases with increasing group size. This phenomenon is well-studied in mammals and birds (Caraco 1979a, 1979b, Caraco et al. 1980, Lima 1987, Elgar 1989, Lima and Dill 1990). Among mammals, the relationship between vigilance and group size has been shown in prairie

dogs (Hoogland 1979), brown hares (Monaghan and Metcalfe 1985), yellow-bellied marmots (Carey and Moore 1986) and ungulates, including bighorn sheep (Berger 1978) pronghorns (Lipetz and Bekoff 1982), mountain goats (Risenhoover and Bailey 1985), Spanish ibex (Alados 1985) and white-tailed deer (LaGory 1986). The same relationship has been observed in many birds, including: starlings (Powell 1974, Jennings and Evans 1980), sparrows (Barnard 1980, Elgar and Catterall 1981, Elgar et al. 1984), finches (Gluck 1986, Popp 1986), juncos (Goldman 1980, Pulliam et al. 1982), swallows (Brown and Brown 1987) tits (Ekman 1987, Hogstad 1988), woodpeckers (Sullivan 1984), geese (Lazarus 1978), ostriches (Bertram 1980), and several shorebird species (Abramson 1979, Metcalfe 1984a, 1984b, Redpath 1988). The vigilance hypothesis has also been supported for characin fish (Godin et al. 1988), minnows (Magurran et al. 1985), and sticklebacks (Van Havre and Fitzgerald 1988).

For some species, the proximity of prey animals in a group may confuse predators by making it difficult to focus their attack on an individual prey item. The “confusion effect” is often used as an example of the antipredator benefits of schooling in fish (Radakov 1973, Hobson 1978). Studies conducted by Neill and Cullen (1974), Major (1978), and Milinski (1979, 1984) support this hypothesis. Hobson (1978) speculates that the confusion effect may be more important for animals in aquatic habitats, where prey are less able to detect predators from a sufficient distance to allow the group to outswim the predator.

Individuals in a group may also reduce their chances of being eaten in two additional ways: by means of predator satiation, or as members of a selfish herd (Harvey and Greenwood 1978, Hamilton 1971). Hamilton (1971) presented the selfish herd

hypothesis as a possible means of protection for prey animals which form close aggregations. In this model, the proximity of each individual animal to its nearest neighbors in the group reduces its chances of being preyed upon. Hamilton's nearest neighbor model was revised in a computer-simulated model generated by Morton et al. (1994). The selfish herd hypothesis has been used to describe aspects of grouping behavior in mammals (Mooring and Hart 1992), birds (Watt and Mock 1987), amphibians (Arnold and Wassersug 1978), and fish (Parrish 1989).

Thus, predation pressure can increase levels of aggregation in many prey animals for many possible reasons. Studies of sociality in mammalian and avian prey species have already presented evidence for several hypotheses describing specific antipredator benefits of group living. Studies have also linked predation pressure to aggregative behavior in arthropods (Treherne and Foster 1980, Dill and Ydenberg 1987, Rasmussen and Downing 1988, Turchin and Kerciva 1989) and fish (Tremblay and Fitzgerald 1979, Pitcher and Wyche 1981, Magurran and Pitcher 1987, Johannes 1993).

Aggregation as an antipredator defense thus far has not been well-studied in reptiles and amphibians (but see Black 1970, Burghardt et al. 1977). Arnold and Wassersug (1978) suggested that aggregations of transforming anurans at the shoreline (such as those observed in *B. boreas*) during metamorphosis may function as selfish herds, in which individuals may decrease their chances of predation by garter snakes. These aggregations may also be large enough to swamp snake predators. Several authors have reported large conspecific aggregations of metamorphosing toads at the edge of the larval habitat (Bragg 1952, Lillywhite and Wassersug 1974, Arnold and Wassersug 1978, DeVito et al. in press).

SYNCHRONY OF VULNERABLE TRANSITIONS

Many animals with complex life cycles undergo transition periods during which they experience increased vulnerability to predation (e.g., Estes 1976, Reaka 1976, Caraco and Pulliam 1984). There are several means by which these animals can increase their chances of survival during these periods (Burghardt et al. 1977, Arnold and Wassersug 1978, Lima and Dill 1990). Most anurans undergo a period of decreased locomotor ability during metamorphic climax (between the eruption of the forelimbs and the complete reabsorption of the tail). The relatively short length of the period of anuran metamorphosis (compared to other life stages) has been suggested to be an evolutionary response to increased predation pressure during metamorphosis (Szarski 1957, Wassersug and Sperry 1977).

Arnold and Wassersug (1978) suggested that synchrony of metamorphosis may function as a method of predator satiation for some frog species. They noted that toads (i.e., *Bufo americanus*), were known to have more synchronous periods of metamorphosis than other sympatric species (i.e., *R. palustris* and *R. sylvatica*). Conspecific synchrony of vulnerable life stages may function as a means of predator satiation for many other taxa (e.g., spawning in fish; Foote and Brown 1997, birth in ungulates; Dauphine and McClure 1974, Estes 1976, juvenile dispersal in lizards; Burghardt et al. 1977, insect metamorphosis; Lloyd and Dybas 1966, Sweeney and Vannote 1982, amphibian metamorphosis; Arnold and Wassersug 1978, DeVito et al. in press, and egg laying in amphibians; Petranka and Thomas 1995).

VULNERABILITY OF ANURAN METAMORPHOSIS

Many anurans are more vulnerable to snake predation during metamorphosis. Wassersug and Sperry (1977) conducted a laboratory experiment in which climax *Pseudacris triseriata* metamorphs were captured by snakes more frequently than tadpoles or juveniles. They also presented evidence that eruption of the forelimbs inhibits aquatic locomotion of metamorphic *P. triseriata*, while the tail remnant inhibits hopping on land. Huey (1980) found that sprint velocity of *B. boreas* tadpoles increased with developmental stage until metamorphosis, when the reduction of tail length led to a decrease in swimming speed. Dudley et al. (1991) found that *Rana catesbeiana* tadpoles reduced swimming behavior and showed a decrease in endurance at the metamorphic climax. These effects were attributed to an unfavorable drag profile associated with the eruption of the forelimbs.

Arnold and Wassersug (1978) examined the stomach contents of *T. elegans* and *T. sirtalis* at several locations in California where the garter snakes feed on metamorphosing *H. regilla* and *B. boreas*. They found a higher proportion of climax (stage 42-45; Gosner 1960) tadpoles in all snake stomachs. In another observational field study, Drummond and Garcia (1989) found that several garter snake species which feed both in water and on land captured more *Rana berlandieri* metamorphs than premetamorphic tadpoles. Drummond and Garcia (1989) also suggested that the spacial distribution may play a role in the vulnerability of metamorphosis, since metamorphosing anurans are concentrated at the shoreline, where they fall prey even to garter snakes that are not aquatic specialists.

SYNCHRONY AND AGGREGATION AS PLASTIC RESPONSES TO PREDATION

To my knowledge, the hypothesis that metamorphic synchrony and aggregation may function as antipredator defenses thus far had only been tested once (Heinen 1993a), and had not yet been supported. It would be difficult to test directly the hypothesis that predation pressure has contributed to synchrony and aggregation over evolutionary time. However, many developmental and behavioral aspects of the amphibian life cycle are plastic characters mediated by environmental conditions, including the presence of predators (Skelly and Werner 1990, Rowe and Ludwig 1991, Sih and Moore 1993, Warkentin 1995). I therefore decided to test the hypothesis that western toads, *B. boreas*, which display metamorphic synchrony and aggregation in the field, would display increased levels of synchrony and aggregation in the presence of a natural predator, the common garter snake (*T. sirtalis*) during metamorphosis. In the laboratory, I tested for an effect of the presence of a snake predator on time to emergence from the water for *B. boreas*, and compared the levels synchrony of emergence and aggregation during metamorphosis.

I then used the same laboratory procedure on a longer timescale to test for an effect of the presence of a snake predator on several aspects of metamorphosis and emergence from the water for the pacific treefrog, *Hyla regilla*, another prey item of *T. sirtalis* (Nussbaum et al. 1983). These variables included: time to metamorphosis and emergence from the water, synchrony of metamorphosis and emergence, and aggregation before and during metamorphosis.

With the results of these two experiments, I could draw conclusions about the plasticity of synchronous anuran metamorphosis and emergence from the water and examine the influence of predators on metamorphic synchrony and aggregation. I could also use these data to analyze the roles of development and behavior in synchronous emergence from the water, and to speculate on the mechanisms responsible for synchronous metamorphosis in the field.

II. EFFECTS OF SNAKE PREDATION ON METAMORPHOSIS OF WESTERN TOADS, *BUFO BOREAS*

INTRODUCTION

Many animals with complex life cycles undergo shifts in habitat, diet, behavior, and selective pressures. These “ontogenetic niche shifts” are often associated with metamorphosis, a period of extensive morphological reorganization (Werner and Gilliam 1984). Metamorphic animals that are no longer suited to their larval environment, and are incompletely suited to their new habitat, might be particularly vulnerable to predation. This is often true for amphibians, and particularly anurans, which pass through a period of decreased locomotor ability as they make the transition from an aquatic herbivore to a terrestrial carnivore (de Jongh 1968; Wassersug and Sperry 1977; Huey 1980; Dudley et al. 1991). For example, some anuran species are most vulnerable to predation by garter snakes (genus *Thamnophis*) near the climax of metamorphosis (Wassersug and Sperry 1977; Arnold and Wassersug 1978, Huey 1980; Drummond and Garcia 1989). The selective pressures associated with the hazards of anuran metamorphosis may have acted to shorten the relative length of this life stage, which may comprise only 15% of larval development (Szarski 1957; Wassersug and Sperry 1977).

Animals have many strategies for dealing with predation during vulnerable life stages. For some species with complex life histories, such strategies may include synchrony of metamorphosis and aggregation of transforming individuals to satiate predators that take advantage of the transition period. Examples include eclosion

synchrony in periodical cicadas and molt synchrony in crustaceans (Lloyd and Dybas 1966; Reaka 1976).

Metamorphic synchrony (temporal proximity in metamorphosis and/or emergence from the water) and aggregation (spatial proximity of individual animals) during emergence from the water have been suggested as possible antipredator adaptations in transforming anurans (Arnold and Wassersug 1978). Terrestrial aggregations of metamorphosing anurans (including *B. boreas*) have been observed at the shorelines of lakes and ponds during emergence (Lillywhite and Wassersug 1974, Arnold and Wassersug 1978, Andrew Blaustein, Jill DeVito, Joseph Kiesecker, Adolfo Marco, personal observations). Possible explanations for grouping behavior of anurans during metamorphosis include antipredator defense (by predator satiation and/or by the selfish herd effect) and protection from desiccation (Lillywhite and Wassersug 1974, Arnold and Wassersug 1978, Heinen 1993a).

Hypotheses to explain synchrony of anuran metamorphosis and emergence from the water include: antipredator defense (by predator satiation), and a mass exodus of tadpoles from drying temporary larval habitats (Arnold and Wassersug 1978). The proximate factors leading to synchronous transformation and emergence from the water are not well understood. The rate of development of amphibian larvae and the timing of amphibian metamorphosis are often plastic responses to many environmental cues including: changes in temperature, water level, density, food availability, and the level of predation (Wilbur and Collins 1973; Werner 1986; Alford and Harris 1988; Newman 1988; 1989, 1992; Crump 1989; Skelly and Werner 1990; Rowe and Ludwig 1991).

Moreover, growth and development can be influenced by the genetic relatedness of individuals (Hokit and Blaustein 1994).

The importance of predation in shaping life histories on the evolutionary scale has long been recognized, but its effect on the life histories of many animals in ecological time has been studied only relatively recently (Sih 1987; Lima and Dill 1990).

Amphibians can respond facultatively to the presence of predators by varying the time or size at which they hatch or metamorphose (Skelly and Werner 1990; Wilbur and Fauth 1990; Sih and Moore 1993; Warkentin 1995).

In this study, we attempt to determine whether a connection exists between predation pressures and the degree of (1) aggregation and (2) synchrony of emergence from the water exhibited by transforming anurans. We conducted a laboratory experiment to test whether the presence of a predator (the common garter snake, *Thamnophis sirtalis*) would affect the level of aggregation of transforming western toads, *Bufo boreas*, and the degree of synchrony with which they emerged from the water.

METHODS

We collected *B. boreas* tadpoles and adult *T. sirtalis* in late July and early August, 1996 at Lost Lake, located in the Oregon Cascade Mountains (Linn County, elevation 1220 m). *T. sirtalis* feed on larval and transforming *B. boreas* during metamorphosis at this site (Andrew Blaustein, Jill DeVito, Joseph Kiesecker, Adolfo Marco, personal observations). The animals were transported to the laboratory, where the tadpoles were

kept in aquaria at approximately 16° C on a 14:10 h light:dark cycle and fed alfalfa pellets *ad libitum* for up to two weeks.

The experiment was conducted in early August at approximately 20° C on a 14:10 h light:dark cycle. We divided 14 plastic tubs (80 cm x 40 cm x 14 cm) lengthwise with nylon mesh screen, filled them with approximately 5 L dechlorinated tap water, and covered them with perforated plastic lids. The tubs were tilted at an angle (approximately 25°) so that half of the floor of each tub was submerged and the other half was completely dry. Five *B. boreas* tadpoles (stage 41, immediately prior to the eruption of the forelimbs; Gosner 1960) were placed on one side of each container. In each of seven experimental containers, we placed a single *T. sirtalis* (SVL = 54 to 87 cm) on the stimulus side of the mesh divider. Throughout the duration of the experiment, toads in the experimental treatments were exposed to a snake for 24 h at a time, every other day. To minimize inter-snake variability, we rotated four snakes between the seven experimental tubs. In all (experimental and control) treatments, we placed one tadpole and one metamorph on the stimulus side of each tub. These toads served as food for the snakes in the experimental treatments. In the experimental treatments, feeder toads that had been eaten by the snakes were replaced during observation periods. The tubs were arranged in a randomized block design.

We recorded the positions of tadpoles (and later metamorphs) at 0800 and 2000 h every day for the duration of the experiment. The toads were considered to have emerged from the water if they were found in the upper third (13.3 cm) of the dry half of the tub, or if they had climbed to the top of the mesh divider, above the level of the water. Toads which had emerged from the water were removed from the tub.

To compare the level of synchrony of emergence exhibited between treatments, we recorded the number of toads removed from each tub during the same observation period. From this we determined the geometric mean (the average number of toads with which an individual toad had emerged) for each toad (Sokal and Rolf 1981). A higher average number of emerging toads per observation period would indicate a higher level of synchrony of emergence.

To compare the level of aggregation between treatments, the proportion of individuals in groups (within one body length of another toad) was recorded for each tub during each observation period. Statistical analyses were performed on the mean values of all observations for each container.

Individuals that emerged from the water were measured, and their snout-vent length and total length were recorded to compare relative tail length (tail length/snout-vent length). Mean relative tail lengths for each tub were used in statistical analyses. To assess whether differences in time to emergence between treatments could be attributed to behavioral or developmental effects, we used multiple linear regression analysis to compare the rates of tail loss between treatments. We would expect that a difference in developmental rates between treatments would correspond with a difference in the rate of tail loss. Conversely, the lack of a difference in the rate of tail loss would indicate a behavioral effect in which tadpoles would attempt to aggregate with conspecifics and/or increase synchrony of emergence by leaving the water at suboptimal stages, either by emerging before locomotion becomes more efficient on land than in the water (i.e., before the loss of the tail; Huey 1980), or by remaining in the water even after losing the tail.

We used multivariate analysis of variance (MANOVA) to test the treatment effect on the tub means of the dependent variables, aggregation, synchrony, and time to emergence (Tabachnick and Fidell 1989). We then analyzed the three response variables individually using independent t-tests with pooled variances. Our Bonferroni adjusted significance level was 0.017 (Zar 1984).

Based on the selfish herd and predator satiation hypotheses, which have been proposed as possible antipredator defenses for transforming anurans including *B. boreas* (Arnold and Wassersug 1978, Lima and Dill 1990), we expected the toads to exhibit a higher degree of aggregation and to leave the water more synchronously in the experimental treatments. Therefore, we used a one-tailed t-test to analyze these effects.

Since the toads used in the experiment were already starting to undergo metamorphosis at the beginning of the experiment, we predicted that a higher degree of aggregation and synchrony would be achieved by a behavioral effect in which metamorphs of slightly different stages would leave the water together in the presence of a snake. Therefore, we expected to find an overall difference between the two treatments in the time taken by the toads to leave the water. This effect was analyzed using a two-tailed t-test.

RESULTS

MANOVA revealed that the presence of the predator *T. sirtalis* had a significant overall effect on the characteristics (time to emergence, aggregation, and synchrony) of *B. boreas* as they emerged from the water ($p = 0.006$) (Table 1). An independent two-tailed

t-test showed that *B. boreas* left the water sooner in the experimental treatments than in the controls ($p = 0.015$)(Fig. 1). Independent one-tailed t-tests showed that the toads (as both tadpoles and juveniles) were more aggregated ($p = 0.017$), and that the metamorphs tended to emerge from the water more synchronously in the presence of the predator ($p = 0.036$) (Fig. 1).

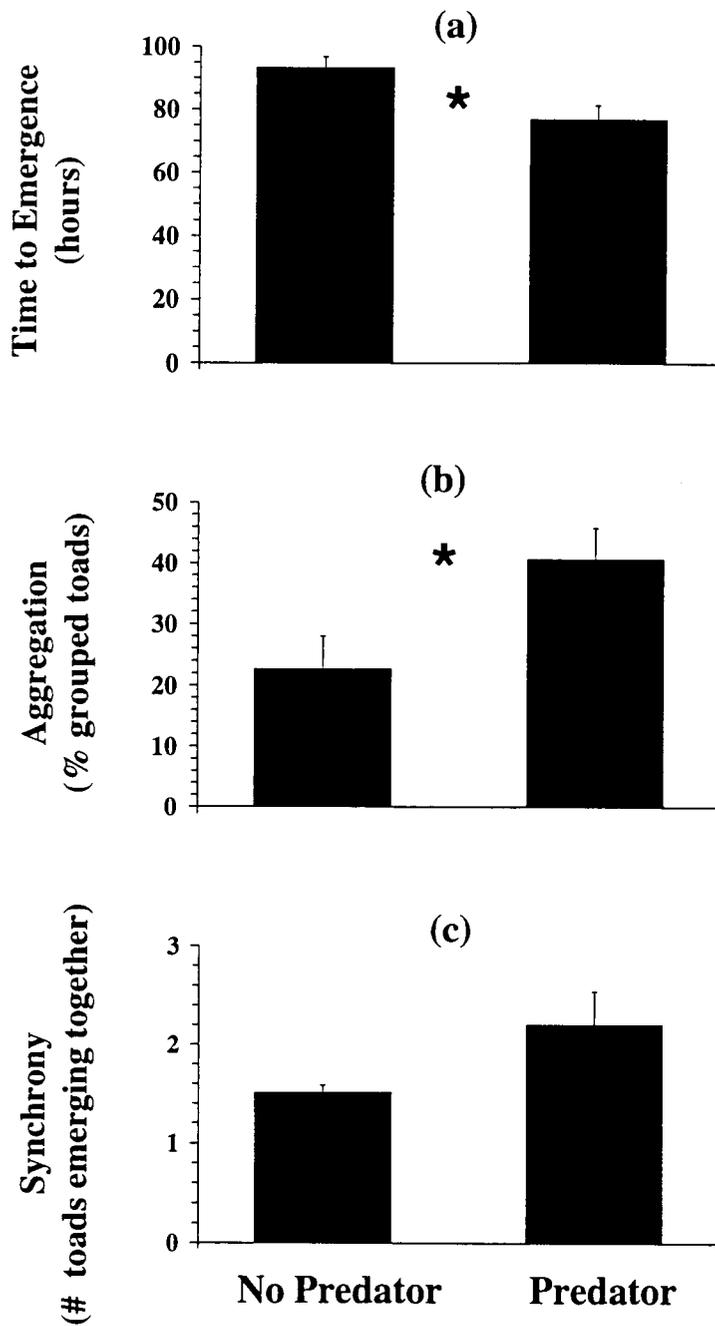
Multiple linear regression showed a significant correlation ($r^2 = 75.29\%$) between tail length (tail/SVL) and time (tail length = $1.17 + 0.118$ time); $p = 0.0001$. The addition of the independent variable, treatment, to the multiple linear regression model did not account for significantly more variation ($p = 0.900$), indicating that there was no difference in the rate of tail loss (i.e., developmental rate) between treatments. This supports the hypothesis that the earlier emergence observed for toads in experimental treatments can be attributed to a behavioral response.

Table 1: Results of MANOVA for overall effects of *Thamnophis sirtalis* on the time to emergence from the water, and levels of aggregation and synchrony of transforming *Bufo boreas* and independent t-tests for each response variable. Response variables are time to emergence, in hours (time), number of toads found in groups (aggregation), and number of toads emerging together (synchrony).

	F	D.F.	P
MANOVA	7.183	3, 10	0.006 (2-tailed)
T-Tests	T	D.F.	P
Time	8.000	12	0.015 (2-tailed)
Aggregation	5.820	12	0.017 (1-tailed)
Synchrony	3.927	12	0.036 (1-tailed)

α for independent t-tests = 0.017 (Bonferroni-adjusted for three response variables).

Figure 1: (a) Mean (\pm SE) time to emergence from the water (hours) for *Bufo boreas* tadpoles, starting from stage 41 (Gosner 1960). (b) Mean (\pm SE) level of aggregation (per cent of toads in each tub found in groups). (c) Mean (\pm SE) level of synchrony (number of toads in the same tub emerging during the same observation period).



DISCUSSION

Our results demonstrate that transforming *B. boreas* show a behavioral response to the presence of a snake predator by controlling their spatial distribution and the time at which they emerge from the water. Metamorphic *B. boreas* emerged from the water sooner, showed higher levels of aggregation, and tended to emerge more synchronously in the presence of *T. sirtalis* than did control animals.

In some species, transforming anurans are captured by snakes more often than larvae or juveniles (Wassersug and Sperry 1977), and evidence suggests that this is the case for *B. boreas* (Arnold and Wassersug 1978; Huey 1980). In the field, aggregations have been observed in transforming toads of many species, including *B. boreas*, and aggregative behavior was suggested by Arnold and Wassersug (1978) as a possible defense against predation by garter snakes. It has also been suggested that transforming anurans may aggregate to prevent desiccation (Black and Black 1969; Arnold and Wassersug 1978). Heinen (1993a) tested the predation and desiccation hypotheses for the aggregation of American toads (*B. americanus*). His results provide evidence to support the desiccation hypothesis for *B. americanus*. Heinen (1993a) also found that juvenile (*B. americanus*) in a completely terrestrial test arena did not aggregate in response to the presence of a snake predator confined in a glass aquarium. However, our results provide evidence that before and during emergence from the water, metamorphosing *B. boreas* aggregate in response to the presence (revealed by visual, chemical, and/or mechanical cues) of snake predators.

Transforming individuals in the experimental treatments may have responded to predator cues by emerging sooner in the presence of snakes regardless of whether they had reached the point in development at which anuran locomotion becomes more efficient on land than in the water. As a result, more toads in the experimental treatment were in the same place at the same time (i.e., on land) when snakes were present. Under natural conditions, this could serve to satiate predators at the shoreline. There may be strong selective pressures on metamorphic toads to remain in the aquatic environment until the point when they can move more effectively on land. This point centers around the loss of the tail, which is the primary means of aquatic locomotion and a major hindrance in terrestrial locomotion (Wassersug and Sperry 1977; Huey 1980). However, if synchrony of emergence is used by metamorphosing anurans as an antipredator defense, there may be opposing selective pressures for an individual to emerge from the water sooner (and with as many conspecifics as possible), whether or not its tail has been lost. Toads which emerge prematurely to reduce predation risk may face alternative threats including an increased susceptibility to dehydration and a decreased thermoregulatory ability (Crump 1989; Lillywhite et al. 1973; Pough et al. 1992).

Because the differential exposure to predators was imposed at the larval stage (41; Gosner 1960) immediately preceding metamorphosis, the higher level of synchrony of emergence and the significant difference in time to emergence exhibited by *B. boreas* in response to the presence of *T. sirtalis* in this experiment could not be attributed to long-term differences in developmental rate. Instead, it appears to be a flexible behavioral response to the presence of a predator. This conclusion is supported by the fact that the linear regression model of tail length over time is not significantly improved by including

treatment as an independent variable; *B. boreas* are not developing (i.e., losing their tails) faster in the presence of predators to emerge from the water sooner.

The metamorphs used in our experiment may have responded to any of the cues to which they were exposed (visual, mechanical, and chemical), but we suspect, based on past experiments in which amphibians have responded to chemical cues (e.g., Kiesecker et al. 1996; Chivers et al. 1997; Flowers and Graves 1997), that a laboratory test performed with only chemical cues (i.e., the scent of the snake, the injured conspecific feeder tadpoles, and the snake feces) might yield the same results as our experiment. However, in the field, metamorphosing toads are faced with a more complex set of stimuli. In a shoreline environment which may be permeated with predator odor, the presence of several cues might be needed to elicit some antipredator behaviors.

Observed behavioral responses of newly metamorphosed toads to the presence of snake predators (on land) include the active choice of cryptic substrates followed by an overall reduction of movement, and engaging in a stereotyped “crouching” behavior (Heinen 1985; Hayes 1989; Heinen 1994a). Hayes (1989) also showed that newly metamorphosed *B. americanus* responded differently to different types of contact by snake predators (i.e., toads attempted to avoid detection by remaining motionless except when contacted by the head of a snake, at which time they attempted to flee).

The presence of snake predators has thus been shown to elicit several short-term behavioral responses in larval and juvenile toads, and we have shown that some of these responses may contribute to the high densities of metamorphosing toads along the shorelines of larval ponds during metamorphosis. However, there may be other (long-term) effects of snake predators on the life-history of *B. boreas*, and some of these may

also contribute to synchrony of metamorphosis. For the majority of larval *B. boreas* in a single habitat to metamorphose within days of each other, the tadpoles must have developed to approximately the same stage over the course of the entire season. It is possible that the presence of predators in the larval environment may influence behaviors affecting the long-term developmental rate of the larval population. Long-term behavioral and developmental responses to predation pressure have been documented for larval *B. americanus* (Skelly and Werner 1990). Morphological changes in anuran larvae have also been observed as an antipredator response (McCollum and Van Buskirk 1996).

One mechanism that may lead to synchrony of metamorphosis is the explosive breeding strategy of *B. boreas*, in which the majority of eggs laid in a particular habitat during any one breeding season are laid within days of each other (e.g., Olson 1989). Another possible mechanism that may facilitate synchronous metamorphosis in the field is the tendency of *B. boreas* tadpoles to travel in large schools throughout the larval period (e.g., O'Hara and Blaustein 1982; Blaustein and Walls 1995). The constant exposure of schooling tadpoles to similar environmental conditions (i.e., water temperature and food supply) may function to keep the developmental growth rate similar among the members of a school. The tendency of some species of toad larvae to aggregate with kin (Blaustein and Walls 1995), and with larvae of similar size (Breden et al. 1982), may also lead to increased synchrony of metamorphosis for schooling tadpoles. Growth and development may also be influenced by the genetic composition of the tadpole schools (Hokit and Blaustein 1994). The movement of larvae in the aquatic environment may also be directly influenced by snake predators; Kiesecker et al. (1996)

showed that larval *B. boreas* from Lost Lake respond to *T. sirtalis* cues by reducing movement and avoiding stimulus areas.

These factors, combined with the short-term responses to predation pressure observed in this study, may allow *B. boreas* to swamp snake predators during metamorphosis. This strategy would decrease the probability of being preyed upon for each transforming toad during the period most vulnerable to predation.

III. EFFECTS OF SNAKE PREDATION ON AGGREGATION AND METAMORPHOSIS OF PACIFIC TREEFROG, (*HYLA REGILLA*) LARVAE

INTRODUCTION

Metamorphosis is a vulnerable transition for many anuran species. During the metamorphic climax (between the eruption of the forelimbs and the reabsorption of the tail; Gosner (1960) stages 42-45), locomotion is inhibited both in the water and on land. The exposed forelimbs increase drag for a swimming metamorph, and the tail remnant inhibits locomotion on land (Wassersug and Sperry 1977, Huey 1980). Several garter snake species (genus *Thamnophis*) which regularly prey on anurans have been observed to take advantage of anuran metamorphosis by aggregating to feed on transforming frogs at the edge of their larval habitat (Arnold and Wassersug 1978, Drummond and Garcia 1989, DeVito et al. in press).

For some anuran species, synchrony (proximity in time) of metamorphosis and emergence from the water may serve as a defense against snake predators (Arnold and Wassersug 1978, DeVito et al. in press). Synchrony of risky transition periods has been suggested as a means of predator satiation in many taxa (Lloyd and Dybas 1966, Dauphine and McClure 1974, Estes 1976, Reaka 1976, Burghardt et al. 1977, Sweeney and Vannote 1982, Petranka and Thomas 1995, Foote and Brown 1997), and relatively synchronous periods of metamorphosis have been observed in the field for several toad species (Bragg 1952, Lillywhite and Wassersug 1974, Arnold and Wassersug 1978). For the western toad (*Bufo boreas*), synchrony of emergence from the water is a plastic response (DeVito et al. in press). The presence of a snake predator (*T. sirtalis*) in a

laboratory setting results in a decrease in the time taken by metamorphosing *B. boreas* to emerge from the water and an increase the level of synchrony of emergence from the water.

Aggregation (proximity in space) of metamorphosing anurans at the edge of the larval habitat may further reduce the chances of predation for each individual (Hamilton 1971, Arnold and Wassersug 1978). Such aggregations have been observed in the field for members of the genera *Bufo* and *Scaphiopus* (e.g., Arnold and Wassersug 1978), and the presence of a predator during metamorphosis increases the level of aggregation of transforming *B. boreas* (DeVito et al. in press).

Both laboratory and field studies present evidence that many anuran species are more susceptible to snake predation during the climax of metamorphosis (Wassersug and Sperry 1977, Arnold and Wassersug 1978, Drummond and Garcia 1989). In the field, Arnold and Wassersug (1978) found higher proportions of climax stage metamorphs in the stomachs of garter snakes (*T. sirtalis* and *T. elegans*) for both *B. boreas* and the Pacific treefrog (*Hyla regilla*). Although the levels of metamorphic synchrony and aggregation observed for *B. boreas* have not been reported for *H. regilla*, we hypothesize that increased synchrony of metamorphosis and emergence from the water should be an appropriate response to the presence of snake predators for many species that are more vulnerable to snake predation during metamorphosis. In this laboratory study, we test the hypothesis that the presence of *T. sirtalis* would influence the development and/or the behavior of *H. regilla* by increasing the levels of 1) aggregation before and during metamorphosis 2) synchrony of metamorphosis (defined by the eruption of the forelimbs; Gosner 1960) and 3) synchrony of emergence from the water.

METHODS

We collected *H. regilla* egg clutches in March, 1997, in a semi-permanent breeding pond outside Corvallis, Benton County, Oregon. We transported the egg clutches to the laboratory, where the larvae were raised in plastic tubs for five weeks at approximately 20° C on a 14:10 h light:dark cycle. Tadpoles were fed alfalfa pellets *ad libitum*. We collected three adult *T. sirtalis* from the same site in early April. Where the two species co-occur, *T. sirtalis* are known to feed on larval, transforming, and adult *H. regilla* (Arnold and Wassersug 1978, Nussbaum et al. 1983).

The experiment was conducted in the laboratory from 21 April to 30 May at approximately 20° C on a 14:10 h light:dark cycle. We divided 10 plastic tubs (80 cm x 40 cm x 14 cm) lengthwise with nylon mesh screen, filled them with approximately 5 L dechlorinated tap water, and covered them with perforated plastic lids. The tubs were tilted at an angle (approximately 25°) so that half of the floor of each tub was submerged and the other half was completely dry. We placed five *H. regilla* tadpoles (stage 26; before the hind limb bud length exceeds 1/2 its diameter; Gosner 1960) on one side of each container. In each of five experimental containers, we placed a single adult *T. sirtalis* on the stimulus side of the mesh divider. The tubs were arranged in a randomized block design. Throughout the duration of the experiment, tadpoles in the experimental treatments were exposed to a snake for 24 hours at a time (0800 h to 0800 h), every other day. To minimize inter-snake variability, we rotated three snakes among the five experimental tubs. In all (experimental and control) treatments, we placed one tadpole on the stimulus side of each tub. These served as food for the snakes in the experimental

treatments. In the experimental treatments, tadpoles or metamorphs that had been eaten by the snakes were replaced during observation periods. Tadpoles were fed alfalfa pellets daily (at 0800 h) throughout the experiment.

Until metamorphosis, we recorded the aggregation level of tadpoles in the water at 0800 h every day. Aggregation level was designated as the proportion of tadpoles found in groups (within one body length (SVL) of at least one other tadpole). During metamorphosis (from the emergence of forelimbs of the first frog to the emergence from the water of the last frog), we recorded the following data at 0800 and 2000 h every day: 1) aggregation of the remaining tadpoles (until only one tadpole remained), 2) time to the beginning of metamorphosis (stage 42, forelimb emergence; Gosner 1960) for each tadpole, and 3) time to the end of metamorphosis (stage 46, complete tail reabsorption; Gosner 1960) for each frog.

Time to emergence from the water was recorded for each juvenile found above the level of the water (on the mesh divider or tub walls). Juveniles were removed from the tubs upon emergence from the water. The stage of each tadpole at emergence was recorded (43, 44, 45, or 46; Gosner 1960) to determine whether any differences in time to emergence could be attributed to a developmental or a behavioral effect. A difference in mean stage at emergence between treatments would indicate a difference in the rate of development between treatments.

Synchrony of metamorphosis and synchrony of emergence were compared using the variances for the mean time to metamorphosis and time to emergence for each tub. Statistical analyses were performed on the mean values of all observations for each container.

Based on the selfish herd and predator satiation hypotheses (Arnold and Wassersug 1978, Lima and Dill 1990) and on the results of DeVito et al. (in press), we expected the frogs in the predator treatments to exhibit a higher level of aggregation in the water, and a higher degree of synchrony of both metamorphosis and emergence from the water.

RESULTS

Tadpoles exposed to snakes showed a significantly higher level of aggregation than the control animals (1-tailed $p = 0.005$) (Fig. 2). However, most of the aggregative behavior observed took place before metamorphosis, and aggregation was not observed outside the water.

Mean time to metamorphosis (566 h) and mean time to emergence (605 h) did not differ between treatments (Fig. 3). The mean stage at metamorphosis (45) did not differ between treatments.

H. regilla emerged from the water one at a time, even in the presence of predators (unlike *B. boreas*, which emerged with more conspecifics in response to the presence of snakes under similar conditions; DeVito et al. in press). However, frogs exposed to snakes exhibited less variance in time to metamorphosis (1-tailed $p < 0.01$) and tended to exhibit less variance in time to emergence (1-tailed $p < 0.1$) than frogs in the control treatment tubs (Table 2) (Sokal and Rohlf 1981).

Table 2: Results of equality of variance test between treatments (predator present vs. no predator present) for mean time to metamorphosis and mean time to emergence from the water of *Hyla regilla* larvae.

	F	D.F.	1-tailed P
Time to Metamorphosis	33.5	4,4	< 0.01
Time to Emergence	4.37	4,4	0.05 < p < 0.1

Figure 2: Mean (\pm SE) level of aggregation for *Hyla regilla* (per cent tadpoles found in groups from the beginning of the experiment until the emergence of the second to last tadpole in each tub). All aggregation took place in the water.

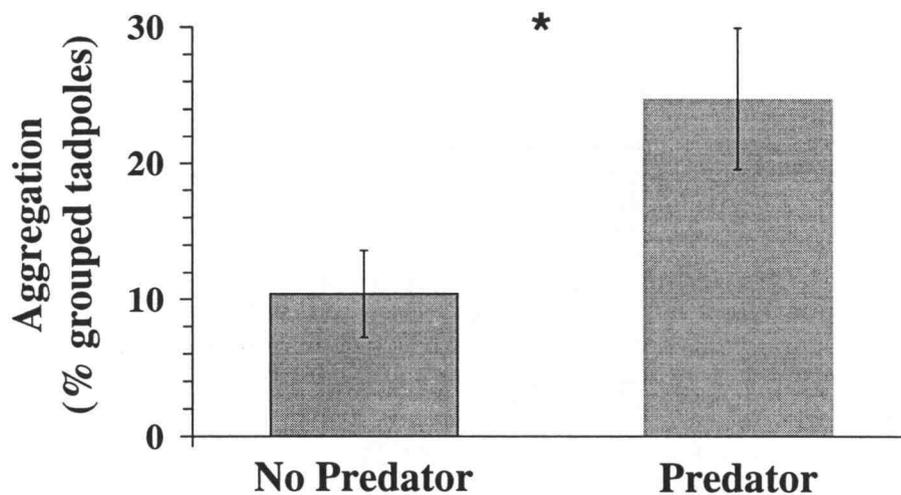
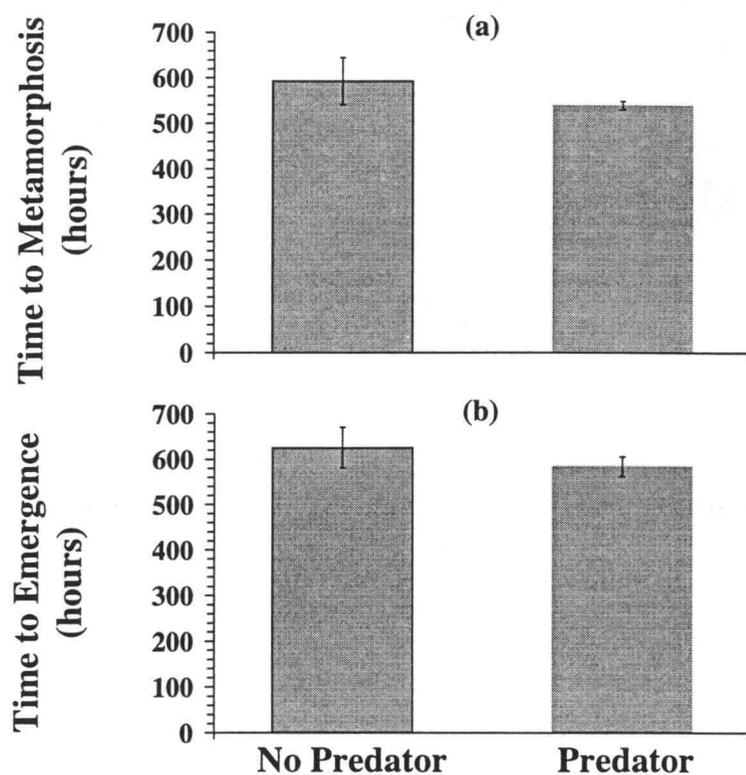


Figure 3: (a) Mean (\pm SE) time to metamorphosis for *Hyla regilla*. (b) Mean (\pm SE) time to emergence from the water. Differences in time to metamorphosis and time to emergence between treatments were not significant. Note the difference in magnitude of standard error bars between treatments.



DISCUSSION

The significant difference between tadpole aggregation levels in predator vs. control treatments supports the hypothesis that the presence of a predator would induce aggregation as an antipredator defense behavior. However, unlike the *B. boreas* subjects of our previous study (DeVito et al. in press) *H. regilla* did not exhibit aggregative behavior during metamorphosis. However, since the majority of juveniles emerged one at

a time, and frogs were removed from each tub upon emergence, the opportunity to aggregate outside the water was limited.

Aggregation of *H. regilla* tadpoles in the laboratory has been reported (O'Hara and Blaustein 1982), but this is, to our knowledge, the first report of increased aggregation of *H. regilla* larvae in response to potential predation pressure. Although schooling in some fish species been cited as an antipredator defense (Neill and Cullen 1974, Major 1978, Milinski 1979, 1984, Johannes 1993), most studies of aggregation in tadpoles have focused on the role of sociality in thermoregulation, foraging efficiency, and development (Bragg 1965, Wassersug 1973, Beiswinger 1975, Breden et al. 1982, Foster and McDiarmid 1982). However, Black (1970) observed aggregation of *Scaphiopus bombifrons* tadpoles in response to the presence of cannibalistic congeners and predaceous insects. Aggregative behavior in the Black (1970) study and in this experiment was induced by predators in the tadpoles of species not normally found in large schools. Future studies should address the role of predation pressure in the behavior of *Bufo* and *Scaphiopus* tadpoles known to travel regularly in large schools (e.g., Duellman and Trueb 1986).

Using the definition of synchrony from our previous study (the number of frogs found out of water in the same observation period; DeVito et al. in press), the results of our study do not support the hypothesis that snake predation would affect the synchrony of metamorphosis in *H. regilla*. However, there was a significant difference in variance of mean time to metamorphosis and a trend toward a difference in variance of mean time emergence between treatments. Thus, if we define synchrony as the magnitude of the variance around the mean time to metamorphosis, the presence of predators in this

experiment increased synchrony of metamorphosis of *H. regilla* and may have also increased synchrony of emergence from the water.

Although there was no significant difference between either the time to metamorphosis or time to emergence from the water between treatments, the last three tubs containing tadpoles at the end of the study were control tubs, and the last tadpoles remaining in these tubs eventually died before transforming. The time to metamorphosis and time to emergence for each of the dead tadpoles was recorded as the observation period time at which the tadpole was found dead. The actual time to metamorphosis and time to emergence for these animals would have been longer (possibly several weeks longer) than the time to death recorded. The mean values of the time to metamorphosis and time to emergence for the control treatments, therefore, were closer to the mean values for the predator treatments than they would have been, had the animals survived to metamorphosis. Although the presence of a predator was not shown to affect the time at which *H. regilla* transform or emerge from the water, we believe that the tendency of the control tubs to contain tadpoles which did not metamorphose indicates a need for further study.

IV. GENERAL DISCUSSION

As described in Chapter I, aggregation as an antipredator defense has been studied for many prey animals. For some prey animals with complex life cycles, conspecific synchrony of developmental processes can provide the opportunity for aggregation during vulnerable life stages. Although very few studies of reptiles and amphibians have addressed the possibility of aggregation in response to predation, chapters II and III present evidence that some larval and metamorphic anurans aggregate in response to the presence of a predator. Furthermore, some anuran species may exhibit increased synchrony of metamorphosis and/or emergence from the water in response to predation pressure.

For anuran species which undergo an ontogenetic niche shift (from aquatic larvae to terrestrial adult) during metamorphosis, the transformation is a risky transition period characterized by a decreased level of locomotor ability and a consequent increase in vulnerability to snake predators (Wassersug and Sperry 1977, Arnold and Wassersug 1978, Huey 1980, Drummond and Garcia 1989). Synchrony of metamorphosis and emergence from the water, along with aggregation during metamorphosis, may defend individuals of some anuran species from predation by garter snakes (Arnold and Wassersug 1978). Evidence for this hypothesis (particularly with regard to *B. boreas*) is discussed in detail in chapters II and III.

Although many studies of prey aggregation in birds and mammals indicate that animals benefit from increased group vigilance (Lima and Dill 1990), Hobson (1978) speculated that the benefits of group vigilance may be greater for animals (i.e., in

terrestrial environments) which are able to flee before being detected by a predator. He suggested that animals (i.e., schooling fish) in environments with limited visibility may benefit less from group vigilance and more from the effect of visually confusing predators. If Hobson's (1978) speculation is accurate, schooling tadpoles escaping from a predator in their natural aquatic environment may benefit from the confusion effect. Metamorphosing anurans, on the other hand, are limited in their ability to flee, both before and after detection by predators (Wassersug and Sperry 1977). Therefore, predator satiation and the selfish herd are probably more reasonable explanations for anuran metamorphic synchrony and aggregation than either group vigilance or the confusion effect.

Many factors affect the optimal time to metamorphosis of amphibians (Wilbur and Collins 1973, Werner 1986). These factors, which vary greatly among species and environments, include: duration of the larval habitat (Crump 1989, Newman 1988, 1989), larval density and intraspecific competition (Crump 1981, Breden and Kelly 1982, Semlitsch and Caldwell 1982, Travis 1984), predation pressure (Werner 1986, DeVito et al. in press), and the degree of plasticity of developmental characteristics (Smith-Gill and Berven 1979, Smith-Gill 1983, Newman 1992).

For metamorphic synchrony and aggregation to be evolutionarily stable strategies, the benefits (of safety in numbers) should outweigh the drawbacks of (1) metamorphosing and/or emerging earlier or later to achieve synchrony with conspecifics and (2) being part of a group. The significant reduction in time to emergence from the water for *B. boreas* in the presence of *T. sirtalis* may have been the mechanism by which *B. boreas* tended to emerge from the water more synchronously in the presence of a predator. Although the

toads may decrease their chances of predation by leaving the water sooner, anurans which emerge from the water at earlier stages and/or smaller sizes may experience difficulties including a decreased ability to thermoregulate, and an increased danger of desiccation (Crump 1989). Drawbacks of aggregation may include an increase in conspecific competition for resources (Petranka 1989), and an increase in probability of detection (of the entire group) by predators (Bertram 1978). For *Bufo* species, these negative aspects should be outweighed by the benefits of predator satiation and/or membership in the selfish herd.

The results of my research suggest that some anuran species (e.g., *H. regilla*) do not exhibit the degree of metamorphic synchrony and aggregation observed for *B. boreas* in response to predation pressure. Wilbur, as reported by Arnold and Wassersug (1978), has observed that toad (i.e., *B. americanus*) populations have more synchronous periods of metamorphosis than other sympatric anurans (i.e., *Rana* species). Also, among anurans, large aggregations of conspecific metamorphosing toads have been reported most often for *Bufo* and *Scaphiopus* species (Bragg 1952, Lillywhite and Wassersug 1974, Arnold and Wassersug 1978). In the short-term experiment described in chapter II, the presence of a snake predator (*T. sirtalis*) induced *B. boreas* to increase levels of aggregation through metamorphosis. Synchrony of emergence from the water also tended to be higher for *B. boreas* exposed to *T. sirtalis* cues. However, by the definition of synchrony used in chapter II, *H. regilla* in the more long-term experiment described in chapter III did not tend to increase synchrony of metamorphosis and emergence from the water in the presence of *T. sirtalis*. Although *H. regilla* increased their level of aggregation in the presence of snakes before metamorphosis, they did not aggregate

during the metamorphic climax. In the following section, I address some possible factors which may make metamorphic synchrony and aggregation more effective defense strategies for some anurans (i.e., *Bufo* spp.) than others (i.e., *Hyla* spp.).

The differences observed between the behaviors of *B. boreas* and *H. regilla* in chapters II and III may indicate that, over evolutionary time, phylogenetic differences have resulted in very different solutions to a common problem--the increased vulnerability to snake predation during metamorphosis. Membership in a group of conspecifics is only one of many anuran antipredator defenses (e.g., Marchisin and Anderson 1978), and may actually preclude other antipredator behaviors (e.g., remaining motionless on a cryptic substrate; Heinen 1994a, 1994b, 1995). The observation that most metamorphosing *H. regilla* in chapter III emerged from the water by climbing vertically suggests that *H. regilla* in a natural setting may climb vegetation and other vertical substrates upon leaving the larval habitat. This could allow some individuals to escape garter snake predation by making detection of *H. regilla* more difficult, or by allowing the frogs to avoid the reach of the snakes.

Juvenile *B. boreas*, on the other hand, are not adept climbers (very few of the individuals in our experiment left the water by climbing the mesh divider, and none were found climbing the smooth plastic sides of the tubs), and although congeneric *B. americanus* metamorphs choose cryptic substrates when possible (Heinen 1993b, 1994b), toads are limited in their ability to avoid the ground-level of the shoreline, where snakes are actively hunting as toads emerge from the water.

The differences between the larval aspects of the life histories of the two species may also lead to differences in metamorphic antipredator defenses. Possible mechanisms

by which toads may achieve higher levels of metamorphic synchrony than other anurans include explosive breeding (e.g., Nussbaum et al. 1983), schooling (e.g., Blaustein and Walls 1995, but see Breden and Kelly 1982), and size-assortative association within schools (e.g., Breden et al. 1982). *H. regilla* are not explosive breeders, and although they associate with conspecifics in the laboratory (O'Hara and Blaustein 1982, DeVito et al. in press), they do not exhibit the level of schooling observed for *Bufo* species (Nussbaum et al. 1983; for discussion of toad aggregation see Beiswinger 1975). They may, therefore, be unable to achieve the levels of metamorphic synchrony exhibited by *B. boreas* and other toad species.

The aggregative behavior of juvenile toads at the shoreline may also be influenced by larval schooling. Lillywhite and Wassersug (1974) suggested that post-metamorphic *Bufo* aggregations may represent a retention of larval behavior. Since *H. regilla* exhibit limited schooling behavior as larvae, they may consequently exhibit lower levels of post-metamorphic aggregation than the juveniles of *Bufo* species.

Most *Bufo* species secrete noxious chemicals which deter many predators (Brodie and Formanowicz 1978, Formanowicz and Brodie 1982, Kruse and Stone 1984, Peterson and Blaustein 1991, 1992). This is another possible factor which may make toads particularly effective at swamping predators during metamorphosis through synchrony and aggregation. Even among snakes, few species (e.g., *Thamnophis*, *Natrix*, and *Heterodon* species) are major predators on metamorphosing toads (Licht and Low 1968), and predator satiation is a more feasible strategy for a species with a limited suite of predators (Arnold and Wassersug 1978). *H. regilla*, on the other hand, is palatable to a

wide range of predators (Nussbaum et al. 1983), so an individual juvenile of the species may not decrease its chances of predation by belonging to a larger group of conspecifics.

While the results of these experiments highlight differences in metamorphic antipredator defenses between *H. regilla* and *B. boreas*, these two species appear to share several common responses to potential snake predation. Although the level of activity of larvae and juveniles was not compared between treatments in these experiments, I qualitatively observed a tendency for metamorphosing *B. boreas* and both larval and metamorphosing *H. regilla* to show minimal activity levels in the presence of snakes. The behaviors described by Heinen (1985, 1994a) and Hayes (1989) for *B. americanus* are consistent with these observations.

Based on past experiments examining the role of chemical cues in eliciting antipredator behaviors in amphibians (Petranka et al. 1987, Hews 1988, Petranka 1989, Sih and Moore 1993, Kiesecker et al. 1996, Chivers et al. 1997, Flowers and Graves 1997), my co-authors and I also suspect that both species examined in this study may respond to the chemical cues of snake predators (direct predator odor, odor of injured conspecific feeder tadpoles, and/or snake feces). Response to the chemical cues of snake predators has been shown for many amphibians (e.g., Petranka et al. 1987, Petranka 1989), including larval *B. boreas* (Hews 1988, Kiesecker et al. 1996) and juveniles of the congeners *B. cognatus* and *B. microscaphus* (Flowers and Graves 1997). The tendency of *H. regilla* larvae to aggregate in response to the presence of snakes in this study may also be the result of predator detection by chemical cues. *H. regilla* respond to the chemical cues of another predator (the bullfrog, *Rana catesbeiana*) in the laboratory (Douglas Chivers, Joseph Kiesecker, Lisa Belden and Andrew Blaustein, in prep.) The role of

chemical cues in inducing earlier emergence of tadpoles from the water and increasing aggregation during metamorphosis should be examined in further studies.

Further experiments should also be conducted to investigate the following questions raised in this study: 1) Does *B. boreas* show not only a short-term behavioral effect of increased synchrony of emergence from the water in response to snake predator cues during metamorphosis, but also a long-term developmental plasticity of synchrony of metamorphosis in response to the presence of snakes? 2) Would the significant differences in behaviors of metamorphosing *B. boreas* between treatments in the laboratory study also be observed in the more complex natural larval environment? 3) Are there differences in the level of plasticity of metamorphic synchrony between populations of *B. boreas* sympatric and allopatric with *Thamnophis* species? 4) What alternative antipredator mechanisms would metamorphosing *H. regilla* display in response to snake predation in the laboratory and in the field? 5) By what means do other anuran taxa reduce predation during the vulnerable period of metamorphosis? 6) Do anuran metamorphs of different taxa exhibit different levels of vulnerability to snake predation? 7) What other (e.g., environmental) factors might play a role in determining the level of vulnerability to predation experienced by metamorphic anurans?

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