

# The development of behavioral defenses: a mechanistic analysis of vulnerability in red-eyed tree frog hatchlings

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I examined the development and effectiveness of behavioral defenses of red-eyed tree frog hatchlings, *Agalychnis callidryas*, against predatory shrimp *Macrobrachium americanum*. Arboreal eggs of *A. callidryas* hatch early if attacked by egg predators and later if undisturbed, producing tadpoles that enter the water at different developmental stages. Older hatchlings survive better than young hatchlings with aquatic predators, including shrimp. Hatchlings respond to shrimp by both increasing activity and avoiding the bottom microhabitat. Older hatchlings are more active and, in the presence of shrimp, avoid the bottom more than young hatchlings. These ontogenetic changes in behavior improve survival. Specifically, the likelihood of fleeing from shrimp increases with hatchling age, and fleeing is an effective defense. In contrast to results from experiments with odonates, immobility does not reduce risk of shrimp attack, thus there is no trade-off between fleeing and motionless crypsis. Shrimp spend most of their time on the bottom, where attacks are more often successful. Avoidance of the bottom microhabitat by tadpoles therefore improves survival. Evasive maneuvers also function in defense, but evasiveness does not change with age. Morphology may limit microhabitat use by younger hatchlings. Failure to flee may reflect unresponsiveness to disturbance, which would reduce unnecessarily early hatching and limit exposure of young *A. callidryas* to aquatic predators. *Key words*: activity, *Agalychnis*, defense, development, *Macrobrachium*, microhabitat, predation, shrimp, tadpoles. [*Behav Ecol* 10:251–262 (1999)]

Growth and development profoundly influence predator–prey interactions (Polis, 1984; Polis et al., 1989; Werner, 1988; Werner and Gilliam, 1984). A widespread pattern is that young animals suffer high predation, and survivorship improves ontogenetically (Polis et al., 1989; Werner and Gilliam, 1984). This common pattern does not, however, have a single underlying cause.

For instance, prey achieve size refuges from gape-limited predators through growth (Brönmark and Miner, 1992; Osenberg and Mittelbach, 1989). Prey develop behavioral, morphological, and chemical defenses against predators (Ash, 1989; Boppré, 1990; Brodie et al., 1978; Dyer, 1995; Formanowicz and Brodie, 1982; Fuiman and Magurran, 1994; Palmer, 1990). Experience or learning also contributes to defense (Chivers et al., 1995; Craig, 1994; Punzo, 1997; Wisendon et al., 1997).

Different defense mechanisms can have different ecological and evolutionary effects. For instance, defenses may protect against multiple predators or protect against one predator at the expense of increased vulnerability to another predator. Selection for defense may be reinforced or opposed by selection for other functions, such as feeding and growth (Anholt and Werner, 1995; Skelly, 1992; Werner and Hall, 1988). Understanding the mechanistic basis of differences in vulnerability therefore aids in interpreting the ecological function and the evolution of defenses.

Amphibian larvae are widely used as model systems for the study of predator–prey interactions. Predation on premetamorphic amphibians typically declines ontogenetically (Calef, 1973; Crump, 1984; Semlitsch and Gibbons, 1988), but the mechanisms by which development reduces predation vary. Growth alone improves survival with gape-limited predators

(Caldwell et al., 1980; Semlitsch and Gibbons, 1988). However, vulnerability also decreases ontogenetically without gape-limitation of predators (Cronin and Travis, 1986; Formanowicz, 1986; Semlitsch, 1990), and without substantial change in prey size (Warkentin, 1995). Amphibian larvae employ a variety of behavioral antipredator defenses, including reduced activity (Anholt and Werner, 1995; Skelly, 1994), increased activity (Hews, 1988), spatial avoidance of predators, and refuge use (Horat and Semlitsch, 1994; Kats et al., 1988; Kiesecker et al., 1996; Petranka et al., 1987). Use of behavioral antipredator defenses may change with development (Bridges and Gutzke, 1997).

Most studies of the ontogeny of behavioral defenses in amphibian larvae have examined swimming performance. Sprint speed typically improves with growth and development and aids in escape from predators (Hoff, 1987; Huey, 1980; Parichy and Kaplan, 1995; Wassersug and Sperry, 1977; Watkins, 1996). However, evasiveness can decline with age (Brown and Taylor, 1995), presumably increasing risk (Feder, 1983; Watkins, 1996). The ontogeny of refuge use has been examined in two species, and in neither could it explain decreasing predation with age (Bridges and Gutzke, 1997; Sih and Kats, 1994).

The study of ontogenetic changes in defense is complicated by the effects of experience. In nature, animals gain experience as they develop. Even under controlled conditions, effects of experience and development are not easily separated. Exposure to predators or predator cues can affect development, such that the morphology of naive prey makes them more vulnerable to predation (Brönmark and Miner, 1992; Harvell, 1990; McCollum and Van Buskirk, 1996; Smith and Van Buskirk, 1995). However, prey exposed to predator cues without mortality may habituate, showing weaker behavioral responses to predators than do naive prey (Bridges and Gutzke, 1997; Jackson and Semlitsch, 1993; Magurran and Girling, 1986). A solution to this problem is to study prey that switch habitats at variable stages of development. This allows a nat-

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ural separation of development and experience, at least with respect to predators restricted to the second habitat.

In this study I examined the development of behavioral antipredator defenses in one such prey, the red-eyed tree frog *Agalychnis callidryas*, specifically addressing the role of prey movement and microhabitat use. Red-eyed tree frogs have a variable period of embryonic development and switch habitats at hatching. *A. callidryas* inhabit lowland, wet forest from the Yucatan through Panama, breeding in temporary ponds and swamps, and sometimes in persistent water such as pools in stream beds. Eggs are attached to vegetation overhanging water, where embryos are threatened by arboreal and aerial predators. At hatching, tadpoles fall into the water where they are threatened by aquatic predators. In Costa Rica, most undisturbed embryos hatch at 7 or 8 days, but when attacked by egg predators tadpoles hatch as early as 5 days (Warkentin, 1995). Late-hatched *A. callidryas* tadpoles are more developed and survive better than early-hatched tadpoles in the presence of both a poeciliid fish, *Brachyrhaphis rhabdophora*, and their most common predator, the freshwater shrimp *Macrobrachium americanum* (Warkentin, 1995). The variation in hatching age in red-eyed tree frogs and the isolation of embryos from aquatic predators allows examination of the effects of development on defense without confounding effects of experience.

This study had two goals. The first goal was to determine which, if any, behaviors serve as antishrimp defenses. The second was to assess the mechanistic basis of the ontogenetic decline in vulnerability, or how tadpole defenses develop. Three experiments were performed to reach these goals. (1) I conducted a predation experiment to determine if the cover-free context necessary for behavioral observations alters the ontogenetic pattern of predation risk. This was necessary because the experiment that demonstrated an ontogenetic decrease in vulnerability of *A. callidryas* to shrimp was performed in a structurally complex environment, in which few behavioral interactions were visible (Warkentin, 1995). (2) I observed the behavior of hatchlings of different ages in the presence of shrimp and in a predator-free context to determine if, and how, tadpoles modify their behavior when exposed to shrimp, and if any such response varies developmentally. (3) I videotaped newly hatched tadpoles interacting with shrimp to determine how tadpole behavior affects shrimp hunting success and how tadpole behavioral defenses change with age.

## METHODS

This research was conducted from 1992 to 1995 under permits from the Costa Rica National Park Service and Ministry of Natural Resources. All experiments were conducted at Sirena Biological Station, in the lowland, wet forest of Corcovado National Park, Costa Rica. All shrimp and young egg clutches were collected from *A. callidryas* breeding ponds and housed in an open-air laboratory. Egg clutches were hung from the sides of plastic tubs containing a small amount of stream water and misted with water daily to prevent desiccation. Shrimp and surviving tadpoles were returned to their collection sites after use.

All experiments compare newly hatched *A. callidryas* (hatchlings) of 4 different ages: 5, 6, 7, and 8 days. Age is measured from oviposition. *A. callidryas* in Corcovado become capable of hatching at 5 days old, and most hatch by age 8 days (Warkentin, 1995). I mechanically induced hatching to obtain hatchlings of each age. Induced versus spontaneous hatching does not appear to alter characteristics of *A. callidryas* tadpoles, and much natural variation in hatching age is induced by egg predators (Warkentin, 1995). To induce

hatching in groups of eggs, I manually jiggled the egg mass and vigorously sprayed it with water. To obtain a single hatchling, I removed an egg from its clutch with forceps and, if necessary, rolled or gently pressed and prodded the egg until it hatched. Most 7- and 8-day embryos and some younger ones hatched without additional stimulation once removed from the clutch.

## Predation experiments

I conducted predation experiments in bowls with and without leaf litter to assess the effect of age on predation in a structurally simple context and to assess the effect of habitat structure on predation. Shrimp were collected 27–29 h before use, housed individually in 250 ml of stream water in plastic cups, and left unfed to standardize hunger levels. This time is adequate for complete gut clearance. I transferred each shrimp to a bowl with 3.25 l of water 2–3 h before experiments began. Bowls were filled with leaf litter to two-thirds water depth for the complex habitat structure treatment and contained a single small leaf as a perch and cover item for the shrimp in the simple habitat structure treatment. Shrimp were  $28.6 \pm 0.3$  mm total length (mean  $\pm$  SE throughout). Only shrimp with both pincers were used. Recently molted shrimp with soft exoskeletons were not used, and replicates with shrimp that molted during the experiment were discarded because shrimp do not hunt while or immediately after molting.

Eggs were induced to hatch in the early evening and equal-aged hatchlings from two to five clutches were pooled. Sets of 12 tadpoles were drawn randomly from this pool and placed in the bowls with shrimp within an hour of hatching. Experiments ran for 24 h. I conducted batches of up to five replicates per age simultaneously, depending on availability of eggs and shrimp. There were 10 replicates without cover (using 5–11 clutches/age) and 5 replicates with cover (using 2–5 clutches/age) for each age. The data on replicates with cover is reported in Warkentin (1995), along with data on predation by smaller shrimp. Effects of age, habitat structure, and their interaction were tested by analysis of variance, with shrimp size as a covariate. Assumptions of normality and homoscedasticity were confirmed with Kolmogorov-Smirnov and Bartlett's tests. All analyses were performed in Systat 5.2.1 (Systat Inc., Evanston, Illinois).

Although this experiment used unequal numbers of clutches per age, an age effect on survival is unlikely to be a spurious result of sibship effects; if anything, uncontrolled sibship effects might obscure an age effect. The effect of habitat structure on predation depends on both the perceptual abilities and hunting techniques of shrimp and the morphology and behavior of tadpoles; thus, uncontrolled differences in morphology or behavior among sibships of tadpoles might obscure an effect of habitat on predation. Hatchling morphology varies little among sibships, although it changes substantially with age (Warkentin, 1998). I tested for an effect of sibship on behavior in the following experiment.

## Behavioral observations

I compared the behavior of hatchlings in the presence of pincerless shrimp with that in predator-free controls across different hatchling ages to assess the development of tadpole behavioral responses to shrimp. Pincerless shrimp provide physical and chemical cues and behaviorally interact with tadpoles but are relatively unsuccessful hunters.

Shrimp readily autotomize pincers; lost pincers regenerate and are complete by the next molt (McVean, 1982). When possible, I collected shrimp that had lost pincers naturally; otherwise I induced pincer autotomy shortly after collecting

the shrimp. Shrimp were housed individually in 2 l of water and fed Tetramin fish food ad libitum. Each shrimp was acclimated to laboratory conditions for at least 26 h and was used 4 times, once with each age of tadpoles, except in 3 cases where shrimp that molted were replaced with new pincerless shrimp. Shrimp were transferred to experimental containers shortly before tadpoles were introduced and were returned to holding containers and fed between experiments. Shrimp were  $32 \pm 0.6$  mm in length.

I divided *A. callidryas* egg clutches into 4 groups of 10 or more eggs shortly after collection ( $n = 10$  clutches). I planned to use one part of each clutch at each age, from 5–8 days. However, some eggs assigned to hatch at 8 days hatched earlier, leaving insufficient 8-day embryos. Other clutches were used to complete the experiment. Tadpoles were observed in bowls filled with 4 l of stream water. Hatching was induced in the early evening, and two sets of five siblings were drawn from each clutch. I placed one set into a bowl with a shrimp and the other into a predator-free bowl within 5 min after hatching. Behavioral observations were made under dim, indirect light to minimize disturbance of the shrimp. I scanned each bowl and recorded positions of all tadpoles 10 times, at 10-min intervals starting 5–10 min after hatching. Tadpole positions were defined as (1) mid-water, not touching any surface, (2) touching the bottom, (3) touching the water surface, or (4) touching the container side. I also observed focal tadpoles for 5-min periods, counting periods of movement (moves) and using a stopwatch to record time spent moving. Focal animal observations were repeated twice per bowl. In each case I chose a focal tadpole that was initially motionless and in the position shared by most other tadpoles in the bowl. In two cases the clawless shrimp caught tadpoles during the experiment; I replaced the missing tadpoles immediately. Data were analyzed using multivariate analysis of variance. Movement data were log-transformed to improve normality and homoscedasticity. Because some 8-day hatchlings were from unrelated clutches, I used only data from 5- to 7-day hatchlings to test if behavior varied among sibships.

### Videotaped predator–prey interactions

#### *Videotape recording*

I recorded and analyzed videotapes of interactions between shrimp and newly hatched tadpoles of different ages to assess developmental changes in tadpole behavior and effects of tadpole behavior on predation by shrimp.

Animal collection and embryo housing were as above. Shrimp were housed individually in round plexiglas tanks 19.1 cm in internal diameter by 15.7 cm deep, filled to 6 cm depth with stream water. Shrimp were acclimated to laboratory conditions for at least 5 days before experiments. During this time they were fed *A. callidryas* hatchlings each afternoon. Experiments commenced once shrimp were feeding well under conditions allowing recording. I measured each shrimp (pincer length, antennae length, and body length, from tail tip to the tip of the rostral horn) either before or after its recording series. Exoskeletal dimensions do not change between molts, and shrimp that molted during the recording process were not used.

Videotapes were recorded at 30 frames/s using a Sony V801 Hi8 videocamera mounted above the tank. A mirror was placed at a 45° angle beside the tank so that a lateral view, providing depth information, was recorded simultaneously with the view from above. A 1-mm grid was placed below the tank and lines marked at 2-cm intervals on the side of the tank for scale. A time trace on individual frames was recorded on the tape. All recordings were of a single shrimp and a

single tadpole in the tank. Although most *A. callidryas* hatch at night (Warkentin, 1995), recordings were made under natural light in the afternoon because shrimp would not hunt at night under artificial light adequate for recording.

Individual eggs were removed from clutches, induced to hatch when necessary, and the tadpoles allowed to fall into the water. Each tadpole was taped for 0–15 min, depending on survivorship. I removed the tadpole and replaced it with another if a shrimp failed to consume it within 15 min. When a shrimp caught a tadpole, I waited 5 min before presenting the next tadpole to ensure that the shrimp was ready to hunt again; shrimp consume tadpoles within a minute. Younger (5 or 6 days) and older (7 or 8 days) tadpoles were presented alternately. If a shrimp neither attacked nor searched for a tadpole within 15 min, it was offered no more tadpoles that day. To control hunger levels, if a shrimp consumed four tadpoles no more were offered that day, and if a shrimp failed to eat at least two tadpoles it was fed embryos to make up the difference after recording was over for the day. Shrimp were offered a maximum of five tadpoles per day.

I recorded three tadpoles of each of the four hatching ages exposed to each of eight shrimp. In three cases, one of the first three tadpoles fell on the shrimp upon entering the water and was eaten immediately. In these cases I recorded a fourth tadpole ( $n = 99$  tadpoles:  $3 \times 4 \times 8 + 3$ ). Experiments used only one tadpole of each age per sibship (24–25 sibships/age).

#### *Videotape analysis*

All interactions between shrimp and tadpoles were examined. Behavioral data were also recorded every 60 s to provide a baseline measure independent of interactions.

Tadpole behavior was categorized as motionless, coasting (moving without beating tail, after swimming), spontaneous swimming (not in response to shrimp, typically slow), or fleeing (sprinting in response to nearby shrimp movement). Shrimp behavior was divided into hunting and other. Hunting shrimp walked or swam with antennae extended or antennal movement and attacked tadpoles they encountered. Most other behavior was resting and grooming.

Three types of interactions were analyzed. (1) Close encounters: shrimp and tadpole came within 4 cm horizontally and 2 cm vertically. In the absence of a behavioral indicator of prey detection independent of attack, I assumed that probability of detection increases with proximity and chose a spatial definition of “close” based on the distribution of a preliminary subset of attack data and on shrimp body size. (2) Attacks: shrimp oriented toward tadpole and approached with pincers extended. I divided attacks into initial and secondary attacks. In initial attacks a shrimp attacked a newly located tadpole. In secondary attacks a shrimp had previously located and attacked a tadpole, which fled, and the shrimp followed and attacked again. (3) Fleeing: tadpole sprinted in response to nearby shrimp movements.

Shrimp position was specified as mouth position, and tadpole position as the center of the body. Positions were measured as height above the bottom and distance from the wall. For interactions, the time, positions of both animals, distance between animals, immediately preceding tadpole behavior, and interaction outcome were recorded. In attacks without a clear initiation point, data were taken for both the earliest and latest possible attack initiation point. For baseline data, position and behavior of both animals were recorded. Distances and positions were measured directly from a monitor against the recorded grid using calipers.

Due to the curvature of the tank, there were two small areas that were not visible in the mirror. Thus for some interactions not all data were obtained. Interactions in these parts of the

tank should not differ systematically from interactions in any other part of the tank. Prior recordings of shrimp and tadpoles in a rectangular tank, in which all interactions were visible in the mirror, indicated an artifactually high mortality rate in the corners (K. M. Warkentin, unpublished data).

#### Analysis of data from videotapes

I tested the hypotheses that tadpole behavior changed with age and that tadpole behavior affected the probability and the success of shrimp attacks. I analyzed 504 attacks, 618 shrimp-induced sprints (fleeing), 375 close encounters, and 795 sets of baseline position data. These included 63 fatalities. To test for developmental differences in tadpole behavior, I averaged behavioral measurements within individual tadpoles, pooled tadpoles across shrimp, and tested for age effects across tadpoles with Kruskal-Wallis one-way ANOVA. I pooled tadpoles within shrimp to test for effects of tadpole behavior on the hunting success of shrimp or survival of tadpoles. For each shrimp, I calculated averages of its successes and its failures, then compared successes with failures across shrimp with a Friedman two-way ANOVA. Using sequential Bonferroni corrections for multiple tests (Holm, 1979), all results remain significant ( $p < .05$ ), except in one case which is noted. I report original significance levels in the results.

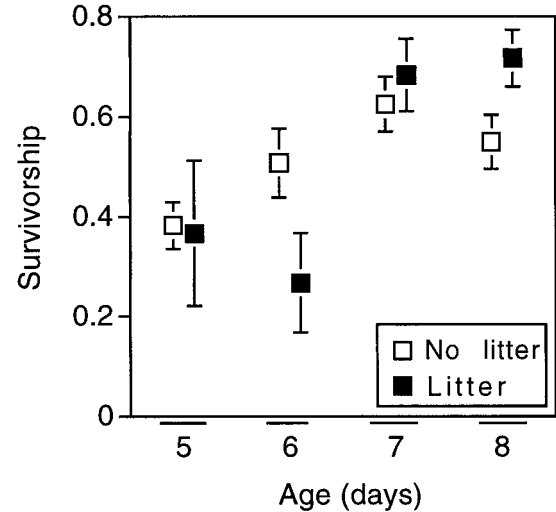
I used only initial attacks to assess factors affecting prey detection because in secondary attacks tadpoles were detected earlier and followed. As a measure of the distance from which shrimp attacked tadpoles in attacks without a clear initiation point, I averaged distances at earliest and latest possible attack initiation ( $n = 94$ , 14 without vertical distance). I combined these averages with measured distances at attack initiation from clear cases ( $n = 285$ , 16 without vertical distance). Using only clear cases gives similar results.

Because shrimp are largely benthic, tadpoles on the bottom may be more frequently encountered and attacked. I determined if the proportion of close encounters and attacks that occurred on the bottom differed from a null hypothesis based on tadpole microhabitat use, using baseline position data (recorded every 60 s) to estimate the tadpole distribution to which each hunting shrimp was exposed.

To assess effect of tadpole movement on shrimp attack, I compared the frequency of initial attacks on motionless and moving tadpoles by nearby shrimp and the distance from which shrimp attacked motionless and moving tadpoles. For attack frequency I examined 375 close encounters, using only cases in which the sequence of attack and sprint, if any, was unambiguous ( $\geq 1/30$  s apart). "Attacked, moving" tadpoles moved before attacked; this includes tadpoles that fled before attacked plus coasting and spontaneously swimming tadpoles. "Attacked, motionless" tadpoles moved only after attacked, if at all. For attack distance, I examined 324 initial attacks. As above, I used average distance in attacks without a clear initiation point.

To test if use of the bottom microhabitat changes ontogenetically, I compared the proportion of baseline position data at 0 cm height across tadpole ages. To test if development affects the likelihood that tadpoles will flee from shrimp, I compared the proportion of times that tadpoles of each age fled in close encounters and in attacks. I compared the number of times tadpoles fled from attacks before capture across tadpole ages for tadpoles caught because they failed to flee. I also calculated the average distance at which each tadpole fled from attacking shrimp (headstart distance), then compared across ages.

I pooled all attacks to estimate the relative importance of position, fleeing, headstart distance, and evasive maneuvers in tadpole survival using partial regression coefficients. For each case, tadpole survival was coded as 1 (survived) or 0 (died).



**Figure 1**

Survivorship of newly hatched *Agalychnis callidryas* tadpoles of different ages over 24 h with a freshwater shrimp in containers two-thirds full of leaf litter (filled squares) or containing a single small leaf (open squares). Data are means  $\pm$  SE for 5 replicates/age with litter and 10/age without litter.

Position (up or on the bottom), evasive maneuvers (performed or not), and fled (or not) were likewise categorical.

## RESULTS

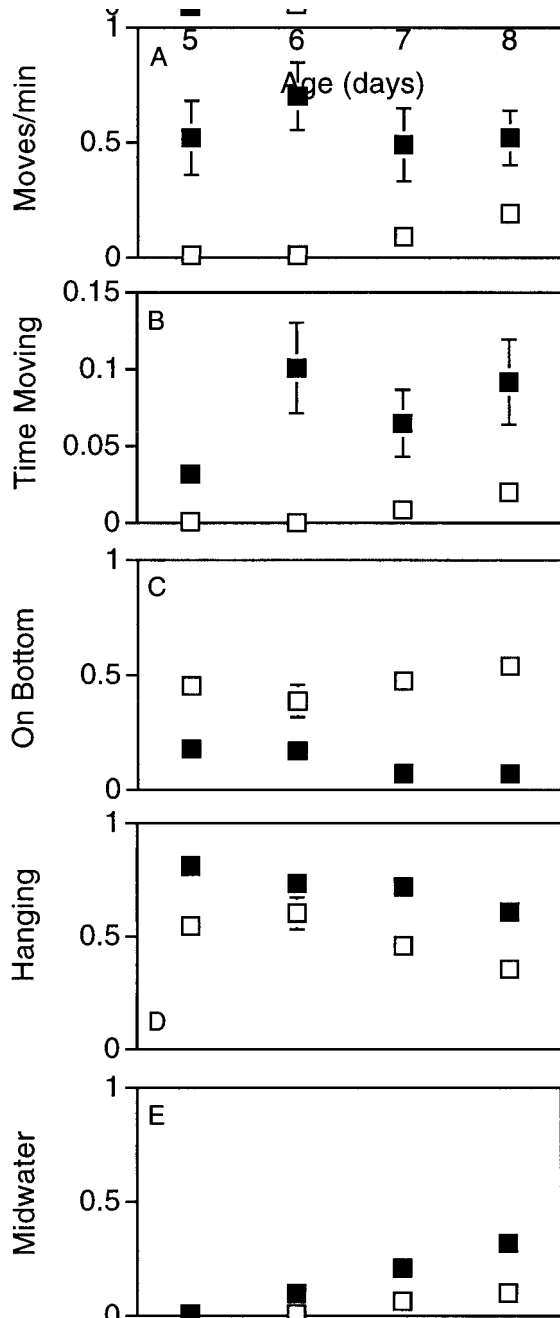
### Predation experiment

Older tadpoles survived better with shrimp than younger tadpoles (Figure 1;  $F_{1,55} = 12.432$ ,  $p = .001$ ). There was no significant effect of habitat structure, either alone or as an interaction with age (Figure 1; structure:  $F_{1,55} = 2.217$ ,  $p = .142$ ; age\*structure:  $F_{1,55} = 2.274$ ,  $p = .137$ ).

### Behavioral observations

Behavior did not vary significantly among sibships (MANOVA for main effect of sibship and all interactions including sibship, all  $p > .27$ ). Tadpoles rested on the container bottom, adhered to the water surface using their external mouthparts, adhered to the container side using mouthparts or cement glands, floated mid-water, or swam. Both tadpole development and the presence of shrimp influenced tadpole activity (Figure 2A,B and Table 1). In the absence of shrimp, tadpoles moved infrequently and spent little time moving. The youngest hatchlings either lay on the bottom (Figure 2C) or adhered to a surface (Figure 2D). Older hatchlings spent a little time floating mid-water or slowly swimming (Figure 2E). In the presence of shrimp, tadpoles moved more frequently and spent more time moving (Figure 2A,B and Table 1). Most movement was sprinting in response to contact with or approach by the shrimp or disturbance by another active tadpole.

There was a significant shrimp-by-age interaction effect on tadpole microhabitat use (Table 1). Tadpoles spent less time on the bottom in the presence of shrimp, and this response was stronger in older, more developed tadpoles (Figure 2C). Reduced use of the bottom is necessarily coupled with increased use of other microhabitats. In the presence of shrimp, older tadpoles increased use of the mid-water microhabitat more than did younger tadpoles (Figure 2E; Kruskal-Wallis test of age effect on change in behavior,  $p = .001$ ). Occasion-



**Figure 2**  
Behavior of newly hatched *Agalychnis callidryas* tadpoles of different ages with freshwater shrimp (filled squares) and without shrimp (open squares). From focal tadpole observations, movement frequency (A) and proportion of time spent moving (B). From scan samples, proportion of observations of tadpoles on the bottom (C), hanging from the surface film or container sides (D), and swimming or floating mid-water (E). Data are means  $\pm$  SE; where error bars are not visible the SE is smaller than the size of the data point.

**Table 1**  
Effects of age and shrimp on the behavior of newly hatched *Agalychnis callidryas* tadpoles: univariate *F* tests from MANOVA

Effect	Behavior	$F_{1,76}$	<i>p</i>
Shrimp	Lying on bottom	.781	.389
	Movement frequency	9.288	.003
	Time spent moving	5.338	.024
Age	Lying on bottom	.067	.796
	Movement frequency	4.662	.034
	Time spent moving	8.016	.006
Shrimp $\times$ age interaction	Lying on bottom	7.821	.007
	Movement frequency	2.951	.090
	Time spent moving	.957	.331

All multivariate test statistics are significant (Wilks' Lambda,  $p = .004$ ,  $.016$ , and  $.001$  for shrimp, age, and interaction, respectively).

ally, 5-day hatchlings at the water surface fell to the bottom; this was never observed in older hatchlings.

#### Videotaped predator-prey interactions

##### Prey detection

Shrimp seldom responded immediately when a tadpole fell into the water, but began antennating a few moments later, and hunting shortly thereafter. Thus tadpoles were detected shortly after they entered the water, although shrimp usually took longer to locate tadpoles precisely. I could not reliably determine when a shrimp had located a tadpole except through its attack behavior: orientation and approach with pincers extended. Often attacking shrimp also folded their antennae back along their body, away from the tadpole.

Most initial attacks occurred when the animals were within 4 cm horizontally ( $68 \pm 5\%$ ) and within 2 cm vertically ( $68 \pm 4\%$ ,  $n = 8$  shrimp; Figure 3). I considered tadpoles within this space close to the shrimp;  $47 \pm 6\%$  of initial attacks were on close tadpoles. Shrimp were  $33.9 \pm 0.99$  mm in total length, with pincers  $18.3 \pm 0.9$  mm and antennae  $43.8 \pm 2.7$  mm ( $n = 8$ ).

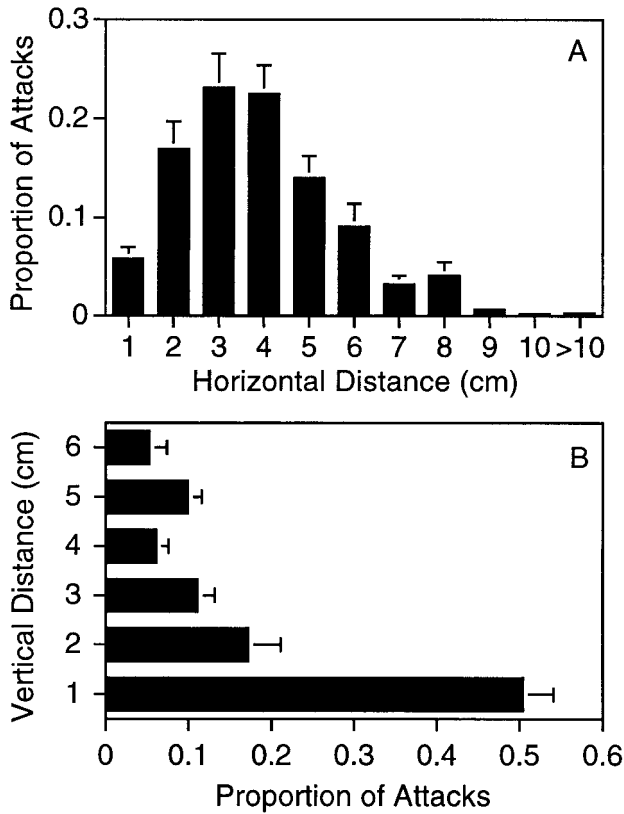
##### Microhabitat use and effect on predation

Tadpoles mostly hung from the water surface or rested on the bottom; they floated and swam mid-water and hung from the sides of the tank less often (Figure 4A). Development affected microhabitat use; younger tadpoles spent more time on the bottom of the tank than did older tadpoles (Figure 4A, and Table 2). Shrimp spent most of their time on the bottom (Figure 4B).

Shrimp did not come close to or attack tadpoles on the bottom ( $\leq 1$  cm up) more often than expected from the proportion of time tadpoles spent there (for both comparisons, Friedman test statistic = 2,  $p = .157$ ). Attacks on tadpoles on the bottom were, however, more often fatal than other attacks (Figure 5 and Table 3). To control for any correlation between tadpole position and fleeing, I considered only cases when tadpoles initially fled. Regardless, shrimp were more successful attacking tadpoles on the bottom (Figure 5, Table 3). Restricting the analysis to cases when tadpoles fled non-stop under pursuit, the trend is nonsignificant (Figure 5 and Table 3), with only six shrimp catching tadpoles.

##### Movement: effect on shrimp attack

Nearby shrimp attacked motionless tadpoles more often than moving tadpoles (Figure 6A). Using a sequential Bonferroni correction for three tests of effects of tadpole behavior on



**Figure 3** Distribution of distances from which shrimp, *Macrobrachium americanum*, attacked newly hatched tadpoles of *Agalychnis callidryas*. Distances were measured between the shrimp's mouth and the center of the tadpole's body. Data are means + SE for horizontal distances (A) and vertical distances (B).

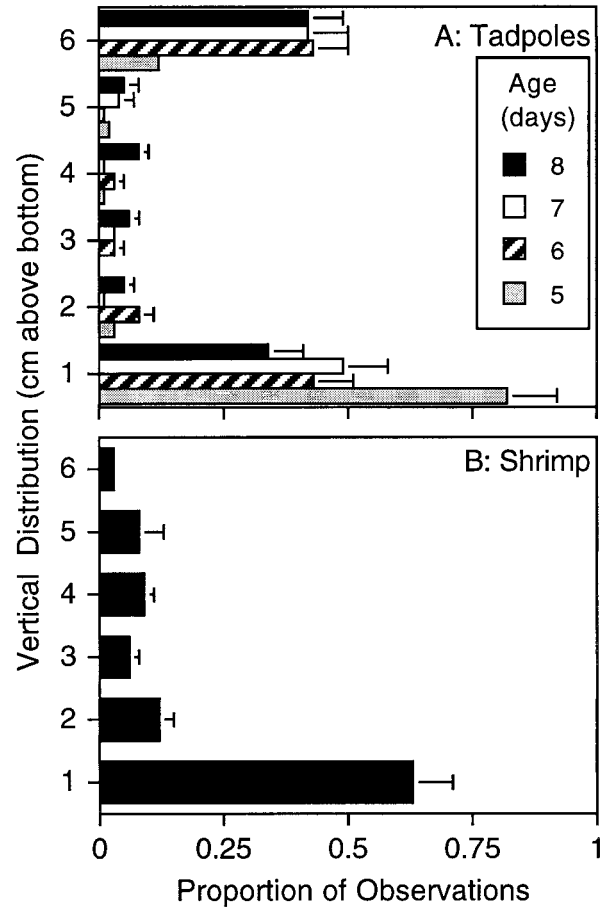
attack probability, this effect is marginally nonsignificant (Friedman test statistic = 4.5,  $p = .034$  versus  $\alpha = .017$ ); however, tadpole movement clearly does not increase the risk of attack by nearby shrimp. There was no significant difference in the distance from which shrimp attacked motionless and moving tadpoles (Figure 6B; Friedman test statistic = 2,  $p = .157$ ).

**Movement: ontogeny**

Older tadpoles more often fled when close to or attacked by shrimp (Figure 7A and Table 2). Older tadpoles fled from more attacks before failing to flee (Figure 7B and Table 2). Older tadpoles also began fleeing at greater distances from the shrimp, giving themselves a greater headstart than younger tadpoles (Figure 7C and Table 2).

**Movement: effect on mortality**

Most mortality occurred when tadpoles failed to flee (Figure 8 and Table 4). Every attacked tadpole that did not flee was caught and eaten. This includes both tadpoles that never fled and those that stopped while being pursued and did not flee again. This 100% success rate of attacks on tadpoles that did not flee contrasts sharply with the  $5.6 \pm 0.9\%$  success rate of attacks on tadpoles that initially fled, and the  $2.5 \pm 0.7\%$  success rate of attacks on tadpoles that fled continuously while pursued (Table 3). Shrimp often did not chase fleeing tadpoles (Figure 8). Even considering only chases, the capture rate was only  $13.0 \pm 4.3\%$  for initially fleeing tadpoles and



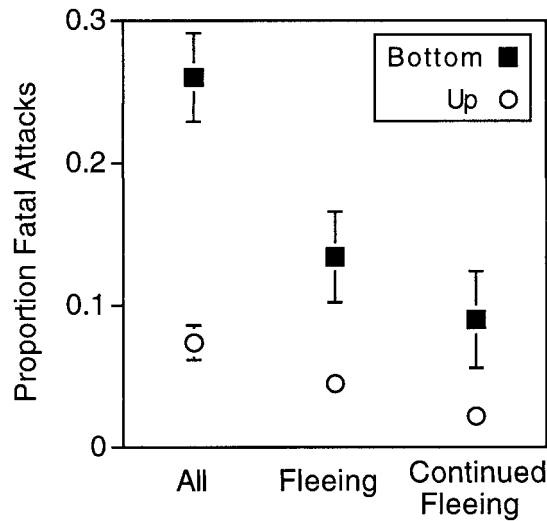
**Figure 4** Vertical distribution of (A) newly hatched *Agalychnis callidryas* tadpoles of different ages and (B) shrimp, *Macrobrachium americanum*. Data are means + SE for proportion of position data in each 1 cm height interval above the bottom, with intervals numbered by upper boundaries. Position data were taken every 60 s for up to the first 15 min of aquatic life for each tadpole. Shrimp positions refer only to hunting behavior. Water depth was 6 cm.

$4.3 \pm 1.1\%$  for tadpoles that continued to flee. There were two cases in which shrimp briefly caught a fleeing tadpole which then immediately escaped their grasp. No motionless or coasting tadpole grasped by a shrimp escaped.

Considering only attacks from which the tadpole fled, the

**Table 2** Effects of age on the behavior of newly hatched *Agalychnis callidryas* tadpoles exposed to predatory freshwater shrimp

Behavior	Kruskal-Wallis test statistic	$p$
Time on bottom	18.073	<.001
Frequency of fleeing when close to shrimp	20.511	<.001
Probability of fleeing when attacked or pursued	17.614	.001
Times tadpole fled before capture without fleeing	18.275	<.001
Evasiveness	3.174	.365
Headstart distance	13.727	.003



**Figure 5**  
Proportion of attacks by freshwater shrimp on *Agalychnis callidryas* tadpoles that were fatal if the tadpole was on the bottom at the start of the attack ( $\leq 1$  cm up; filled squares) or up off the bottom at the start of the attack (open circles). Data are means  $\pm$  SE for all attacks ( $n = 8$  shrimp), attacks only on tadpoles that fled ( $n = 7$ ) and attacks only on tadpoles that fled and continued to flee while pursued ( $n = 6$ ).

headstart distance of tadpoles in fatal attacks was less than their headstart distance in nonfatal attacks (Figure 7C and Table 3).

Tadpoles that fled and were followed by shrimp made evasive maneuvers, defined as sudden changes of direction (Feder, 1983; Watkins, 1996) 21.2 $\pm$ 4% of the time. The chance of making such maneuvers did not change significantly with age (Table 2). Chasing shrimp were more likely to cease following tadpoles that made evasive maneuvers, compared with tadpoles that did not (Figure 8 and Table 3).

#### Which behavior most affects survival?

Fleeing explained much of the variance in survival and was clearly more important than any other factor. In a model including fleeing and position,  $r^2 = .755$  and standardized regression coefficients were .857 and .050, respectively ( $n = 488$  cases). For a second model including position, headstart distance, and evasion and using only cases where the tadpole fled ( $n = 392$ ),  $r^2 = .031$  and coefficients were .095, .128, and .049, respectively.

Figure 8 summarizes the sequence of tadpole and shrimp behavior following an attack, showing the ways in which tadpoles escaped or were caught. By far the most common cause of death was failure to flee. In contrast, tadpoles that fled usually survived. On average 50% of tadpoles that fled were not chased (56.3 $\pm$ 8% for initial attacks). Infrequent evasive maneuvers strongly affected a tadpole's chance of escape: shrimp pursued tadpoles through only 11% of evasive maneuvers versus 67% of nonevasive fleeing. Nonetheless, relatively few tadpoles were caught while fleeing. In many cases tadpoles stopped or slowed to coasting while still pursued. A substantial number were caught because they were attacked again and failed to flee. Others fled again and many were not chased; stopping and fleeing again was slightly but not significantly more effective in escaping shrimp than just continuing to flee (45.3 $\pm$ 11% versus 33 $\pm$ 12% escaped, Friedman test statistic = 2,  $p = .157$ ).

**Table 3**  
Effects of behavior of *Agalychnis callidryas* tadpoles on the success of attacks by freshwater shrimp

Tadpole behavior	Friedman test statistic	$n$	$p$
Position (on bottom vs. off bottom; all attacks)	8.000	8	.005
Position (only initially fleeing tadpoles)	7.000	7 <sup>a</sup>	.008
Position (only tadpoles that continued to flee)	2.667	6 <sup>a</sup>	.105
Fleeing (initial)	8.000	8	.005
Fleeing (continued)	8.000	8	.005
Evasive maneuvers	7.000	7 <sup>a</sup>	.008
Headstart distance	7.000	7 <sup>a</sup>	.008

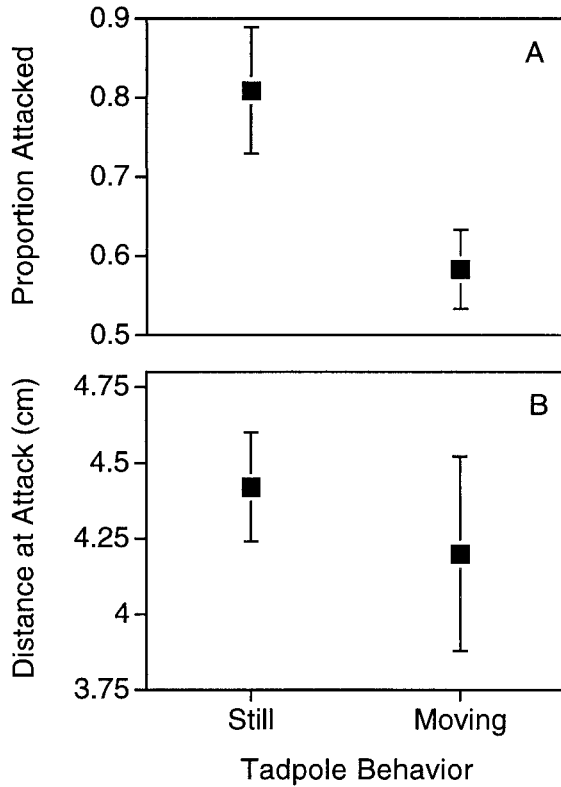
<sup>a</sup> Reduced sample sizes reflect parameters that could not be compared for particular shrimp. Two shrimp failed to catch any continuously fleeing tadpoles, thus position effects on their attack success in such cases are irrelevant. For exposure to one shrimp, no tadpoles performed evasive maneuvers.

#### DISCUSSION

The overwhelming factor affecting survival of red-eyed tree frog tadpoles in the presence of shrimp is whether or not the tadpoles flee when attacked. By far the majority of tadpoles that flee escape predation. In contrast, I found no evidence that tadpoles that fail to flee ever escape. Tadpole activity does not increase the risk of shrimp attack; if anything, the risk is reduced. Thus tadpoles exposed to shrimp do not face a trade-off between remaining motionless to avoid attack and swimming away to avoid capture. Likewise, there is no trade-off between activity-dependent feeding and an inactivity-dependent defense. This is in sharp contrast to most studies of tadpoles with odonate predators, where complete immobility substantially improves survival by reducing risk of attack, fleeing appears less important, and a feeding versus defense trade-offs exists (Anholt and Werner, 1995; Chovanec, 1992; Skelly, 1992, 1994, 1995; Skelly and Werner, 1990; Werner, 1991; Werner and Anholt, 1996). Even with odonates, however, increased activity sometimes reduces predator success (Hews, 1988).

Because habitat complexity did not alter tadpole survivorship, leaf litter should not be considered a refuge from shrimp, and it is reasonable to examine behavioral defenses in a structurally simple environment. Also, because cover does not reduce mortality of the youngest, least active tadpoles, the failure of immobility as a defense in the videotaped interactions cannot be attributed to lack of cover. Shrimp forage actively and will eat plant material and scavenge as well as attack live prey (Garces and Heinen, 1993; New, 1976). Food searching and grasping are elicited by chemical stimuli in a congener (Harpaz and Steiner, 1990), and in *M. americanum* prey detection and recognition are clearly not dependent on movement. Given the low frequency with which pursuing shrimp catch fleeing tadpoles, the average energetic gain may be low, and the energetic costs of attack and pursuit may select against such behavior. In contrast, the 100% success of attacks on tadpoles that fail to flee makes attacking motionless tadpoles advantageous.

Younger tadpoles flee from shrimp attacks significantly less often than do older tadpoles; 8-day hatchlings fail to flee in only 4% of attacks, whereas 5-day hatchlings fail to flee in almost half (Figure 7A). This difference seems sufficiently large to explain the roughly twofold higher mortality of 5- versus 8-day tadpoles in predation experiments. Indeed, the

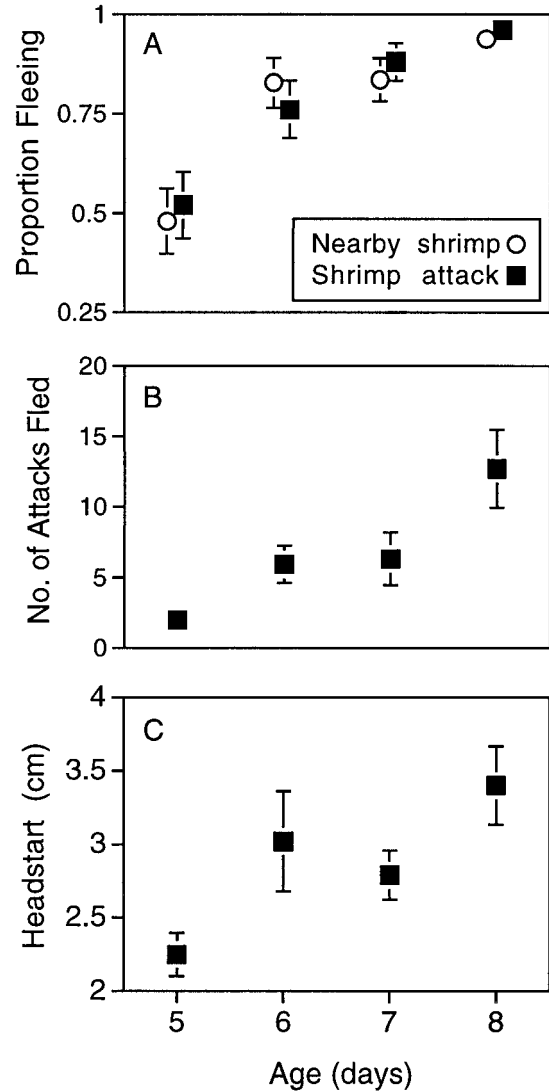


**Figure 6**  
Effect of movement by *Agalychnis callidryas* tadpoles on attack by freshwater shrimp. (A) Proportion of times that nearby shrimp (at or within 2 cm vertically and 4 cm horizontally) attacked motionless and moving tadpoles. (B) Distance from which shrimp attacked motionless and moving tadpoles. Data are means  $\pm$  SE;  $n = 8$  shrimp.

lower mortality of older tadpoles is largely due to fewer “failed to flee” fatalities (Table 4).

Other factors explain relatively little of the variation in survival, but still differ significantly between fatal and non-fatal attacks. Tadpoles on the bottom are less likely to survive shrimp attacks than are tadpoles in other locations (Figure 5). This could contribute to improved survival for older hatchlings because the proportion of time spent on the bottom declines with development. Although shrimp spend most of their time on the bottom, I did not detect an effect of position on likelihood of attack; shrimps on the bottom swam up to attack tadpoles above them. My experimental design probably underestimates the importance of position because tadpole–shrimp interactions were videotaped in water only 6 cm deep, and many *A. callidryas* breeding ponds are much deeper. Microhabitat use of shrimp and *A. callidryas* hatchlings in the wild parallels that in my tanks; shrimps use the bottom and other substrates, and hatchlings mostly lie on the substrate or hang from the water surface (K. M. Warkentin, personal observation). In deeper water hatchlings at the surface are much farther from shrimp on the bottom than they were in my experiment, which may reduce attack probability.

Although *A. callidryas* tadpoles infrequently perform evasive maneuvers (sudden changes of direction), such maneuvers dramatically increase the likelihood of escape from pursuing shrimp (Figure 8, Table 3). Evasive maneuvers are also important in the escape of tadpoles from garter snakes and turtles (Feder, 1983; Watkins, 1996). These predators, like shrimp and unlike odonates, are active foragers that chase tadpoles. Evasiveness of red-eyed tree frog tadpoles did not

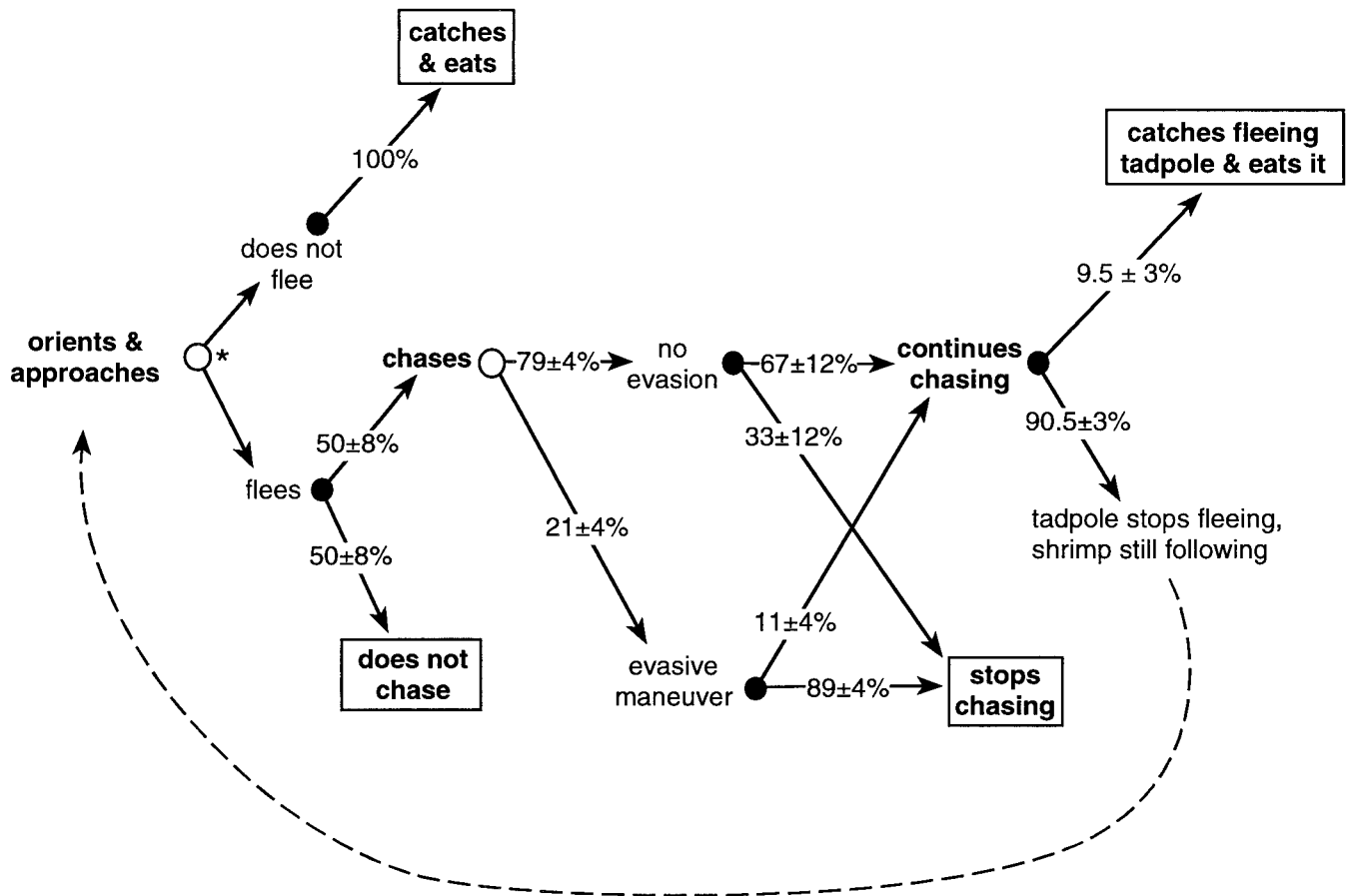


**Figure 7**  
Effects of development (age) on fleeing by newly hatched *Agalychnis callidryas* tadpoles with predatory shrimp. (A) Proportion of times that tadpoles fled from nearby shrimp (at or within 2 cm vertically and 4 cm horizontally; open circles) or from attacking and pursuing shrimp (filled squares). (B) For tadpoles that failed to flee when attacked or under pursuit, and so were eaten, the number of attacks from which they had previously fled and survived. (C) Headstart distance of tadpoles fleeing from shrimp attacks. Data are means  $\pm$  SE.

change developmentally, and so evasiveness does not contribute to the lower mortality of older hatchlings.

Hatchlings respond behaviorally to shrimp in two ways that reduce mortality. First, tadpoles of all ages are more active in the presence of shrimp (Figure 2A,B). Increased activity is largely due to tadpoles fleeing from shrimp, which clearly reduces the success of attacks and may also make attack less likely. Second, tadpoles of all ages reduce use of the bottom microhabitat in the presence of shrimp, and this response is stronger in older tadpoles (Figure 2C). I detected a relatively weak effect of tadpole position on attack success, but in deeper water tadpoles may also avoid attacks by avoiding the bottom, and other substrates.

The ontogenetic change in microhabitat use may be influenced by three aspects of development—specifically lung and



**Figure 8**

Sequence of behavioral interactions for freshwater shrimp, *Macrobrachium americanum*, preying on newly hatched *Agalychnis callidryas* tadpoles. Boldface type and filled circles indicate shrimp behavior. Light type and open circles indicate tadpole behavior. Probabilities of alternative transitions are given as means  $\pm$  SE. \*The probability of fleeing depends on tadpole age, ranging from  $52 \pm 8\%$  at 5 days to  $96 \pm 1\%$  at 8 days. This set of behaviors accounts for all 326 escapes and all but 8 of 63 recorded captures. The excluded captures are three in which the tadpole fell on the shrimp when entering the water and five when the tadpole swam into the shrimp.

tail growth and differentiation of external mouthparts (Warkentin, 1998, in press). Lung size in *A. callidryas* embryos increases substantially from 5 to 8 days, allowing older hatchlings to achieve neutral and even positive buoyancy, whereas 5-day hatchlings consistently sink (Warkentin, 1998). To avoid the bottom and other substrates, negatively buoyant young tadpoles must either swim or adhere to the water surface. The smaller tails of 5-day hatchlings may hamper swimming performance, and their less developed mouthparts sometimes fail to adhere to the water surface (Warkentin, 1998). Thus bottom-avoidance is more energetically costly for younger tadpoles, and morphology appears to limit behavior.

The cause of the ontogenetic change in propensity to flee from shrimp is less obvious. Because there is no trade-off between avoiding and escaping attacks, natural selection by shrimp predation is directional and favors fleeing. Why do the youngest hatchlings flee so infrequently? I consider three hypotheses. (1) Not fleeing is adaptive; other, stronger, selection pressures in the water oppose selection by shrimp predation and favor immobility. (2) Not fleeing reflects developmental limitations. (3) Not fleeing is a pleiotropic effect of selection on embryos.

Although tadpole immobility increases predation by shrimp, it might be advantageous in a larger context. Specifically, other predators may selectively prey on active tadpoles. Odonates and other sit-and-wait predators are likely candi-

dates for such agents of selection. Shrimp, however, are by far the most abundant predator of tadpoles in the study area, with dense populations in most *A. callidryas* breeding sites (Warkentin, 1995). As well, in preliminary experiments shrimp ate more tadpoles per capita than did other invertebrate predators. Poeciliid fish co-occur with and prey on *A. callidryas* tadpoles in some breeding sites (Warkentin, 1995). However, most poeciliids are omnivores and, like shrimp, will readily consume immobile food items (Meffe and Snelson, 1989). More importantly, if inactivity truly confers a net benefit, why are older hatchlings so active? Because of the delayed hatching of undisturbed clutches, young *A. callidryas* are less likely than older animals to be in the water. Selection on tadpoles in the water should thus be more effective on later stages.

A variant of the first, adaptive, hypothesis is that selection pressures on tadpoles change with age such that immobility confers a net advantage only for the youngest hatchlings. This could occur if fleeing were a less effective defense for younger tadpoles. The frequency with which fleeing tadpoles were captured declined slightly with age; however, even fleeing 5-day hatchlings were captured only 6.6% of the time. Compared with the 100% mortality of nonfleeing tadpoles, an opposing selection pressure would need to be extremely strong for failure to flee to be an adaptation to aquatic conditions. There are no obvious candidates for such a strong selection pressure.

A second hypothesis is that failure to flee results from in-

**Table 4**  
**Distribution of mortality and escapes of *Agalychnis callidryas* tadpoles attacked by freshwater shrimp, *Macrobrachium americanum***

	Frequency/age (days)				% of fatalities or escapes
	5	6	7	8	
<b>Fatality type</b>					
Did not flee when attacked	16	7	3	4	47.6
Stopped under pursuit, did not flee again	2	5	6	3	25.4
Caught while fleeing	3	2	3	1	14.3
Swam into shrimp	1	1	1	2	7.9
Fell on shrimp as entering water	1	2	0	0	4.8
Total fatalities	22	17	15	10	100
<b>Escape type</b>					
Not chased when fled <sup>a</sup>	27	47	55	79	63.8
Escaped sprinting	13	27	15	22	23.6
Escaped in evasive maneuver	6	13	12	10	12.6
Total escapes	46	87	82	111	100

Each of eight shrimp was offered three tadpoles of each age, except in three cases when a tadpole fell on the shrimp entering the water, when an additional tadpole was offered.

<sup>a</sup> Includes cases in which tadpoles under pursuit stopped, then sprinted again and were not chased, as well as cases in which shrimp did not chase the initial sprint.

complete development of sensory and motor systems, not direct selection. The youngest tadpoles may simply not be sufficiently developed to consistently detect or respond to approaching shrimp. Nonetheless, these tadpoles did flee from shrimp attacks half the time, suggesting that they do detect shrimp and can respond, and even the youngest hatchlings have well-developed neuromasts and eyes (Warkentin, 1998).

A third hypothesis is that selection pressures on embryos may oppose those on tadpoles, making young hatchlings less likely to flee than they otherwise would be. An undisturbed arboreal egg clutch is a safe place, much safer than most ponds for small, young tadpoles. Undisturbed clutches do not hatch at 5 days, and few undisturbed embryos hatch at 6 days; most wait until 7 or 8 days (Warkentin, 1995). If remaining in a safe egg is favored through 7 days, younger arboreal embryos should not hatch in response to minor disturbances such as wind, rain, or spiders walking on them; indeed, they do not (Warkentin, 1995).

Rapid early hatching is a behavioral response to disturbance by egg predators. *Agalychnis callidryas* embryos are attached to vegetation by tough, elastic jelly. In removing eggs from the clutch, predators create a substantial disturbance that induces rapid hatching (Warkentin, 1995). *A. callidryas* hatch by vigorous movements that rupture the egg membrane; motionless embryos do not hatch. The hatching movements appear similar to the escape response of posthatching larvae, as in fish (Eaton and Nissanov, 1985). This suggests that escape hatching and fleeing from aquatic predators may share an underlying sensory and motor mechanism, a common neuromuscular pathway. If so, selection against unnecessarily early hatching might reduce sensitivity or responsiveness of this pathway in younger embryos, with correlated effects on the response of young hatchlings to aquatic predators. After locating a motionless tadpole, shrimp often approach slowly and do not touch the tadpole until the fatal strike. In such cases the vibratory cues transmitted to the tadpole must be substantially weaker than the disturbance to embryos during snake attack. Selection by aquatic predators on young hatchlings for increased sensitivity to disturbance would fall only on the fraction of tadpoles actually in the water at that stage, those just attacked in the egg. Older animals are more likely to be in

the water, thus selection by aquatic predators would be more effective at later ages, and we expect older hatchlings to be better adapted to aquatic life.

The importance of fleeing as a defense against predatory shrimp contrasts strikingly with the defensive role of inactivity with odonate naiads (Anholt and Werner, 1995; Skelly, 1994). Clearly, behavioral defenses are not universally effective; behavior that improves survival with one predator can seriously reduce survival with another. Thus the efficacy of putative defenses must be considered in the context of an entire suite of predators, and particular behaviors should not be considered defenses without predator-specific demonstration of their effectiveness. When different predators impose opposing selection pressures on prey defenses, prey may evolve specific responses to different predator types. Such response specificity is known in primates (Cheney and Seyfarth, 1990) and in birds (Evans et al., 1993). Some amphibian larvae also distinguish among predators, responding behaviorally only to those predators against which the behavior functions in defense (Lefcort, 1996), and showing stronger responses to more dangerous predators (Kiesecker et al., 1996). Only by recognizing the often restricted effectiveness of antipredator defenses will we be able to determine to what extent multiple predators have shaped prey phenotypes and how conflicting selection pressures generated by different predators affect both response specificity of prey and their ecological interactions with a suite of predators.

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