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BEHAVIORAL INTERACTIONS BETWEEN THE GIANT WATER BUG (*BELOSTOMA LUTARIUM*) AND TADPOLES OF *BUFO WOODHOUSII*

Charles C. Swart[1,*] and Ryan C. Taylor[1]

ABSTRACT - The relationship between predator and prey is dependent on resource availability, the predators' hunting strategy, the prey's suite of antipredatory mechanisms, and the complexity of the habitat. We conducted a laboratory experiment to evaluate background preferences by tadpoles of *Bufo woodhousii* Girard and the predaceous water bug *Belostoma lutarium* Stål (Hemiptera: Belostomatidae). Our results indicate that 1) tadpoles switched preference away from black backgrounds when a chemical signal from *B. lutarium* was introduced, 2) earlier stage tadpoles exhibited a stronger effect than later stage tadpoles in the presence of the predator's chemical signal, 3) hemipterans were observed randomly on both backgrounds but were mostly found associated with vegetative cover, and 4) *B. lutarium* killed significantly more tadpoles on dark backgrounds compared to light backgrounds.

INTRODUCTION

Life history (Stearns 1992) and optimal foraging theories (Charnov 1976) share the central concept of tradeoffs between time spent foraging and predation risk. Both theories predict that prey species should evolve mechanisms which allow them to respond in a manner that maximizes overall lifetime fitness (Chase 1999; Werner and Anholt 1993, 1996). Balancing the benefits of foraging against the risk of predation has been shown to be an important driving force in habitat selection (Storfer et al. 1999, Turner et al. 2000), growth rates (Chase 1999, Skelly 1992), size at adulthood (Wilbur 1997), and fecundity (Chase 1999, Lima and Dill 1990, Sih 1987). This relationship holds for a diversity of taxa including fishes (Dahlgreen and Eggleston 2000), amphibians (Babbit 2001, Babbit and Jordan 1996, Kupferburg 1998), insects (McPeek and Peckarsky 1998, McPeek et al. 2001), birds (Cresswell 1999), and mammals (Kotler and Brown 1999).

Species at significant risk of predation mediate this pressure by altering behavior, microhabitat selection, or morphology. These induced defenses (Tollrain and Harvell 1999) are effective at mediating predation pressure, but they also lead to higher order effects, such as increased or reduced growth rate, body size, fecundity, or population growth rates (Chase 1999, Storfer et al. 1999, Werner 1992, Werner and

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Anholt 1993, Wilbur 1997). The size and direction of the higher order effects depend on the particular characteristics of the predator and prey species as well as the characteristics of the environment, including habitat complexity, competition, and food availability (De Meester et al. 1994, Hopper 2001, McPeek 1998, McPeek and Peckarsky 1998, McPeek et al. 2001). Thus the dynamics of predator prey interactions of one particular species pair may not apply to other species pairs, even among closely related species or different populations of the same species. A lack of empirical data on specific predator and prey behaviors during predation events hampers the ability to predict these higher order effects (Lima and Dill 1990, Luttbeg and Schmitz 2000).

Among amphibians, predation pressure is highest in the aquatic juvenile stages, and a limited number of induced defenses have been described, including motionlessness, crypticity, tail morphology alteration, and cover use (Babbitt and Jordan 1996, Kupferberg 1998, Skelly 1994, Van Buskirk et al. 1997). The most common response of larval amphibians to predation pressure is motionlessness, often used in conjunction with other antipredator mechanisms. However, to our knowledge, the prediction that crypsis should reduce the reliance on motionlessness has not been tested (Lima and Dill 1990). Life history models predict that motionlessness reduces growth rates and causes a shift in the growth/predation response curve favoring metamorphosis at a smaller size (Werner 1986, Werner and Anholt 1993). Vegetative cover use is another important antipredator defense employed by tadpoles. While vegetation is important in reducing the predation rate of stalking or benthic predators, it is not effective against belostomatids (Hemiptera, *Belostoma*) that are lie-in-wait predators and are always associated with emergent vegetation (Babbitt and Jordan 1996). Previous studies on growth rate of larval amphibians have yielded conflicting results, depending on resource availability or the presence of lie-in-wait predators (Babbitt and Jordan 1996, Werner and Anholt 1996).

Melanic tadpoles of Woodhouse's toad *Bufo woodhousii* (Anura; Bufonidae) forage on light-colored sand/silt substrates, dark-colored leaf litter, or around submergent and emergent vegetative cover in ponds or slow moving bayous across the southcentral and southwestern United States. Their most common predators are adults and larval aquatic insects (belostomatid water bugs, dytiscid beetles, odonate larvae; Roth and Jackson 1987). Predaceous water bugs of the genus *Belostoma* (Hemiptera) are typically found associated with vegetation or leaf litter near the shore of aquatic habitats. Belostomatids are air-breathing insects that hold their respiratory siphons above the surface while using vegetation as perches. At our field site, they are among the most common predacious insect encountered when collecting tadpoles, and they readily feed on toad larvae in the laboratory (pers. obs.).

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We report the results of a study designed to determine how closely the antipredator tactics of larval *Bufo woodhousii* are coupled with the predation tactics of *Belostoma lutarium*. We designed two laboratory experiments to determine the role of chemical signaling, antipredatory behavior, and background matching in interactions between tadpoles of *B. woodhousii* and their predator *B. lutarium*. In the first experiment, we tested the predictions that tadpoles would change their preference for background association or cover use in the presence of a chemical signal from the hemipteran. In the second experiment, we tested the prediction that tadpole chemical signals would affect background association in *Belostoma*.

While the identity of the chemical signals involved in this predator-prey relationship are not specifically identified, previous work has identified four chemical signals produced in the cephalic glands of the belostomatid, *Abedus herberti*(Lokensgard et al. 1993). These 21 carbon steroidal compounds are thought to deter fish predation on *A. herberti*.

METHODS

Tadpoles of *B. woodhousii* and adults of *B. lutarium* were dipnetted from near-shore environments where they co-occur in a large slow moving bayou (Little Wauksa Bayou, Saint Landry Parish, Louisiana). The tadpoles were dense at the site of capture (about $40/m^2$) in near-shore environments. Belostomatids (about $3–5/m^2$) were associated mainly with near-shore submergent and emergent vegetation but were also captured in the leaf litter at the bottom of the pond at lower densities ($< 1/m^2$). Adult *B. lutarium* and larval *B. woodhousii* were captured between 5 and 15 July 2000, returned to the laboratory at The University of Louisiana at Lafayette, and maintained in separate containers (480 ml cups) under a 12:12 hour day:night light cycle until testing. Tadpoles were identified with the key of Altig (1970) with verification of species from metamorphosed specimens. Tadpoles were partitioned into developmental stages immediately after each trial according to Gosner (1960) stages. All *Belostoma lutarium* were identified using the key characters of Lauck (1964). Voucher specimens of *B. lutarium* are maintained at the Louisiana State Arthropod Museum, Baton Rouge, Louisiana. Specimens of the emergent plant *Eclipta alba*, commonly found at the field site, were collected from a nearby cypress swamp. All specimens were housed and tested at room temperature (about 21°C).

Experiment 1

This experiment was designed to test the prediction that tadpoles of *B. woodhousii* would adjust background matching or refuge usage in the

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presence of a predator's chemical cue. The effect of tadpole developmental stage and activity of the tadpole was also tested. Plastic translucent containers (15 x 25 x 12 cm) were filled with 1 L of dechlorinated water and each housed a single tadpole. The containers were placed on top of construction paper, black (7.5 x 12.5 cm) on one half and white (7.5 x 12.5 cm) on the other half. The black and white sides were randomly alternated between sides among replicates. No tadpole was used in more than one test.

Two treatments were applied and each was replicated 32 times. Treatment 1 included the addition of 20 ml of dechlorinated water (control) to the center of the container and a piece of plant material (*Eclipta alba*) for a refuge in the center of each background color. Treatment 2 was identical to treatment 1 except that 20 ml of predator treated water was added in place of the dechlorinated water. A stock solution of predator treated water was made by mixing water from several containers that had housed a *Belostoma* for at least 24 hr immediately prior to the test.

Test chambers were placed on a covered shelf with dimensions 1 m wide by 3 m long. The observer was shielded from the test chamber by a wall of black plastic. Observations were made through 5 cm slits in the plastic. Flourescent lights were mounted within the enclosure but the room lights were turned off during testing. Four replicates of each treatment were run simultaneously in eight trials over a 5-day period. One tadpole was introduced to the middle of the container and allowed to acclimate for 0.5 hr before an experimental treatment was added. Thereafter, a reading of tadpole position was taken every 5 min for 20 readings (100 min). The developmental stage of each tadpole was recorded after each trial.

To control for acclimation to the presence of the chemical signal, a chi-square test was used to compare the mode of the first 10 observations to the mode of the last 10 observations. For both treatments, each tadpole's choice of background was taken to be the mode of the 20 observations.

Experiment 2

This experiment was designed to test the prediction that belostomatid water bugs would shift their use of background color or use of refuge sites in response to a chemical signal from prey. The same apparatus used in experiment 1 was used in this experiment, except in this case a single belostomatid was housed in the experimental container. Three treatments were applied. Treatment 1 was identical to treatment 1 in experiment 1. Treatment 2 was identical to treatment 2 in experiment 1 except that 20 ml of water from a cup in which a tadpole had been living for 24 hours was used (tadpole treated water). Treatment

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3 was identical to treatment 2 except that a tadpole was introduced to the middle of the chamber instead of 20 ml of tadpole treated water. Each treatment was replicated 28 times. A total of 65 hemipterans were used. Some bugs were used in two treatments, but none that were exposed to a chemical signal or to a live tadpole in the first trial was used again. Our field observations indicated that *Belostoma lutarium* is always associated with emergent vegetation or leaf litter debris.

RESULTS

Experiment 1

To test for habituation to the chamber over time, we tested whether the use of background color by tadpoles (in treatments 1 and 2) in the first 10 observations was significantly different from the final 10 observations. A paired t-test indicated that there was no significant difference in background choice ($t_{(2,62)} = -0.719$, $P = 0.477$). We used a log-linear model to analyze the data on tadpole responses to hemipteran chemical cues. A log-linear model is a contingency table used to analyze binomially distributed data. We chose a log-linear model because we could not satisfactorily transform the data to meet the assumptions of ANOVA. In addition, log-linear models test explicitly for interactions among factors, something that is not possible with an aligned rank ANOVA. Two factors were used in the analysis, chemical cue (presence or absence: treatment 2 versus 1) and tadpole stage. The response variables examined were cover use and background choice. We initially constructed a full log-linear model where we examined the effects of chemical cue and tadpole stage on background choice and cover use by tadpoles. We then systematically decomposed the full model to find which factors yielded the most parsimonious explanation of the data (Feinberg 1980).

The analysis revealed that hemipteran chemical cues had a significant effect on background use by tadpoles ($\chi^2_1 = 7.92$, $P = 0.0049$). Tadpoles chose black backgrounds significantly more often in the absence of hemipteran chemical cues than in the presence of such cues. In the presence of hemipteran chemical cues, tadpoles increased their use of white backgrounds such that they used black and white backgrounds with nearly equal frequency (Fig. 1A).

The use of background color by tadpoles was significantly different among stages ($\chi^2_1 = 3.99$, $P = 0.046$). In the absence of hemipteran chemical cues, early Gosner stage tadpoles (< stage 34) spent the majority of their time on black backgrounds. However, in the presence of hemipteran chemical cues they spent nearly equal amounts of time on black and white backgrounds. Later Gosner stage tadpoles (> stage 35)

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spent nearly twice as much time on black backgrounds regardless of whether or not hemipteran chemical cues were present (Fig. 1B). Despite differing background choices by younger and older stage tadpoles, there were no significant interaction effects among chemical cue and tadpole stage on background choice ($\chi^2_1 = 0.05$, $P = 0.8280$).

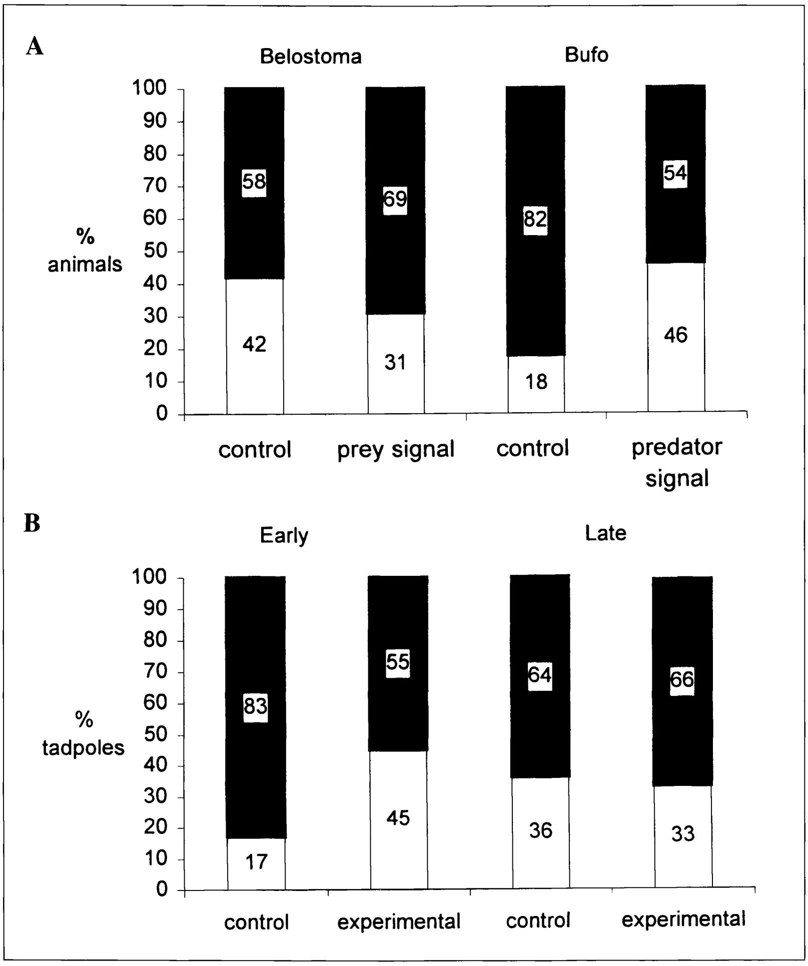

Figure 1. (A) Background preference of (left) *Belostoma lutarium* and (right) tadpoles of *Bufo woodhousii*. Left portion shows the hemipterans' choice of background (black or white) with chemical cues from tadpoles present and absent ($\chi^2_1 = 3.87$, $P = 0.052$). Right portion shows tadpoles' background choice with chemical cues from hemipterans present and absent ($\chi^2_1 = 5.76$, $P = 0.023$). (B) Background preference of early stage (< Gosner stage 35) versus late stage (> Gosner stage 34) tadpoles of *Bufo woodhousii* ($\chi^2_1 = 3.99$, $P = 0.046$). Left portion shows the early stage tadpoles choice and right portion shows late stage tadpoles choice of background (black or white) with chemical cues from water bugs present and absent.

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Tadpoles spent significantly more time away from cover objects than they did under cover objects ($\chi^2_1 = 57.83$, $P < 0.0001$; treatments 1 and 2). This occurred regardless of whether hemipteran chemical cues were present or absent. Only two tadpoles used cover objects during the experiment.

As a measure of movement by tadpoles under different treatments, we compared number of changes between background colors by tadpoles in treatment 1 (control) and treatment 2 (hemipteran chemical). Results of a t-test indicate no significant difference in movement between the two treatments ($t_{(2,62)} = -0.637$, $P = 0.527$). Likewise a t-test revealed no difference in movement between early stage tadpoles (< Gosner stage 34) and late stage tadpoles (> Gosner stage 35; $t_{(2,62)} = -0.973$, $P = 0.334$).

Experiment 2

As in the first experiment, we tested for habituation effects. We tested whether the use of background color by hemipterans (treatments 1 and 2) in the first 10 observations was significantly different from the last 10 observations. A paired t-test indicated that there was no significant difference in background choice ($t_{(2,54)} = 1.357$, $P = 0.186$).

A log-linear model was used to determine if hemipterans changed their use of cover and background color when encountering the chemical signal of tadpoles. They did not change their use of background color in response to chemical cues from tadpoles ($\chi^2_1 = 3.87$, $P = 0.052$). In the absence of tadpole chemical cues (treatment 1), hemiterans chose black backgrounds in 58% of observations and white backgrounds in 42% of the observations. In the presence of tadpole chemical cues (treatment 2), they shifted their use of black backgrounds to 69% of observations versus 31% on white backgrounds. Likewise, there was no significant difference between the use of cover by hemipterans in the presence or absence of tadpole chemical stimuli ($\chi^2_1 = 0.16$, $P = 0.685$). The presence or absence of chemical cues from tadpoles also did not make a significant difference in the number of times hemipterans changed position between black and white backgrounds ($t_{(2,54)} = 1.599$, $P = 0.116$).

In our predation treatment 3, we tested whether the number of successful captures by hemipterans differed by background. A Chi-square analysis revealed that they captured significantly more tadpoles on black backgrounds than on white backgrounds ($\chi^2_1 = 4.765$, $P = 0.029$).

DISCUSSION

Motionlessness, or reduced activity, is employed by numerous anuran larvae as an antipredator defense (Babbitt and Jordan 1996,

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Kupferberg 1998, Skelly 1994). However, we failed to detect a difference in activity between our experimental and control treatments for experiment 1, but larval *Bufo woodhousii* did alter background choice from black to white in the presence of belostomatid chemical cues. Furthermore, younger tadpoles accounted for most of this effect. From the second experiment, tadpoles were killed more on dark backgrounds, but we do not have data on the stages of these tadpoles. Current data on the ontogentic effect of size as a refugium from predation suggest that older, larger larvae are less vulnerable to predation (Werner and Gilliam 1984) as demonstrated with *Bufo americanus* and the predatory *Anax junius* (Anholt et al. 1996)

Our test chambers were constructed to mimic the dark and light substrates available to these animals in their natural habitat. Belostomatids are nearly always associated with dark-colored substrates in near-shore environments and in vegetation and leaf litter. Tadpoles can be found in these dark-colored substrates (leaf litter, vegetation, algal mats) where presumably foraging is most productive, and they are also present in light-colored sand, silt substrates, where they are visually conspicuous. Few tests of background choice among amphibians are available, but larval salamanders (*Ambystoma barbouri)* prefer backgrounds that most closely match their own color, especially in the presence of a predator (Storfer et al. 1999). Furthermore, tadpoles of *Xenopus laevis* exhibit a shift in preference from light to dark background during ontogeny (Moriya et al. 1996). In larval *Xenopus laevis*, the ontogenetic change in preference for background color changed from dark to light as the larvae developed melanocytes (Moriya et al. 1996). No ecological relationship was suggested for *Xenopus*, and all larval *Bufo* that we used had well developed melanic coloration.

Our results indicate that younger tadpoles may escape predation pressure from *Belostoma* by shifting habitats when a chemical signal of the predator is detected. *Bufo* may reach a size refugium as seen in other anurans (Kehr and Schnack 1991, Werner and Gilliam 1984) or may develop toxic skin glands that limit their risk of predation (Crossland 1998). Crossland showed that older tadpoles of *B. marinus* (with well developed skin glands) are toxic to *Lethocerus indicus* (Belostomatidae) in Australia, although no mortality was observed in our animals. It has been suggested that predators with piercing mouthparts may overcome this defense (Wassersug 1973).

Several previous studies have shown an advantage to use of vegetation by tadpoles under predation pressure (Lima and Dill 1990). Our results indicate that the opposite may be true when lie-in-wait predators commonly occur in vegetation. If food resources are found primarily on

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the dark substrates, belostomatids may limit growth rate of young tadpoles through habitat shifts rather than through reduced activity of tadpoles as seen in other anuran studies with different predators (e.g., dytiscids and odonate naiads: Roth and Jackson 1987, Van Buskirk et al. 1997). Similar results were found by Babbitt and Jordan (1996) with tadpoles of *Bufo terrestris* and *Belostoma flumineum* and by results of Figiel and Semlitsch (1991) with crayfish (*Procambarus acutus*) and tadpoles of *Hyla chrysoscelis*.

Whereas the time lost in foraging is a cost commonly associated with the use of motionlessness as an anuran anti-predator defense, the cost to larval *Bufo woodhousii* could be both time lost foraging while on light (less vegetation) backgrounds, as well as susceptibility to other predators caused by increased visual conspicuousness when on light-colored backgrounds. Belostomatids killed more tadpoles on black than on white backgrounds, and larval *Bufo* apparently shifted to a white background in response to this predatory effect in our experiment. Previous work with tadpoles of *Rana temporaria* suggest that plasticity in antipredatory behavioral responses are effective defenses against predators with different hunting tactics (Laurila 2000). *R. temporaria* larvae avoided the fast swimming European perch, *Perca fluciatilis*, using motionlessness, but avoided the slower predatory dragonfly larvae, *Aeshna juncea* by maintaining a long distance between itself and the source of chemical signals from the predator.

The tradeoff between time spent foraging and anti-predator behavior, in most systems studied to date, would predict increased survival of tadpoles in areas with adequate vegetative cover. Lie-in-wait predators such as *Belostoma* may alter this prediction, particularly if they are present in large numbers as seen in our field site (and generally in all vegetated ponds across the southeastern United States). One possible antipredator defense against this type of predator is switching to non-vegetated areas, as suggested by our data. The potential costs incurred are time lost from foraging in richer habitats and, in the case of melanic bufonid tadpoles, potential conspicuousness to other predators in non-vegetative, light-substrate areas.

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