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Factors Affecting the Predator-Prey Relationship Between Predaceous Diving Beetle Larvae (Dytiscus fasciventris) and Two Anuran Tadpole Species (Bufo americanus and Hyla crucifer)

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Anuran Tadpole Species (Bufo americanus and Hyla crucifer).

(TITLE)

BY

Todd S. Campbell
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THESIS

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ABSTRACT

It has previously been demonstrated that American toad
(Bufo americanus) tadpoles are more vulnerable to predation
by diving beetle larvae (Dytiscus fasciventris) than are
spring peeper (Hyla crucifer) tadpoles. A laboratory study
was undertaken to further delineate factors that contribute
to the differential vulnerability observed. Beetle larvae
are more effective tadpole predators in shallow, than in
deep, water and appear to prefer to adopt a "sit-and-wait"
predator strategy while clinging to emergent vegetation.
Depth preference experiments in the laboratory indicated
that both tadpole species prefer deep areas to shallow
areas irrespective of whether a predator was present or
absent. Dytiscus preferred the shallow end (0 - 5 cm of
water) of the depth choice tank when tadpoles were absent,
but preferred deeper areas when tadpoles were present.
Beetle larvae prefer to eat in shallow areas, or on
vegetation near the water surface. Both tadpole species
appear to be more vulnerable to predation on light colored
substrates, indicating that vision may be a more important
prey locating mechanism in beetle larvae than previously
thought. Bufo tadpoles move significantly more than Hyla
tadpoles, which results in a higher vulnerability for Bufo.
Field experiments show a positive relationship between
tadpole density and the number of tadpoles a beetle larva
is able to capture. Field results also suggest that late

stage *Bufo* tadpoles (which move the same amount *Hyla* tadpoles do) are not more vulnerable to beetle larvae than are *Hyla* tadpoles, further delineating the relationship between the amount of movement tadpoles exhibit and the level of tadpole vulnerability to beetle larvae. These results are discussed with reference to some evolutionary theories of predator-prey systems.

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INTRODUCTION

The complex life cycle of anurans has been the subject
of many aspects of ecological research (see Wilbur, 1980
for a review). Tadpole populations occur most frequently
in springtime temporary or semi-permanent ponds with rapid
primary production and significant time lags in the
appearance of aquatic predators. They delay somatic and
reproductive development in favor of growth in order to
exploit the extensive primary production of ephemeral ponds
(Wassersug, 1974).

A wealth of literature has recently emerged addressing
the conflicting roles of predation and competition in
shaping tadpole community structure (see Morin, 1983).
Studies by Brockleman (1969), DeBenedictus (1974), Woodward
(1982), Alford and Wilbur (1985), and Wilbur and Alford
(1985) have formulated a strong argument for the role that
competition plays in dictating anuran larval community
structure.

Other studies indicate that predator-tadpole
interactions lower tadpole densities enough to eliminate
the effects of competition (Calef, 1973; Heyer et. al,
1975; Heyer, 1976). Cecil and Just (1979) found that
populations of small (< 20 mm) Rana catesbeiana tadpoles
are controlled primarily by invertebrate predation, and not
(at least as much) by abiotic factors or food availability.
The outcome of competition in larval anuran communities may

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depend on the density of predators present, and in the absence of these predators, the relative species abundance may be reversed in relation to species abundance when predators are present (Morin, 1983). In some cases, entire guilds may be eliminated by predators.

Another hypothesis currently being advanced is that many factors, including predation, tadpole density, order of hatching, competition, and food availability are collectively responsible for the regulation of tadpole guild composition (Wilbur, 1972; Morin, 1983; Travis et al., 1985a). For example, Neill (1968) found that different survivorship curves for gulf coast toad tadpoles (Bufo valiceps) were due to a combination of insect (dytiscid) predation and tadpole competition. Likewise, larval distributions of striped chorus frog larvae (Pseudacris triseriata) on Isle Royal, Michigan were said to result from the interactions of permanence of larval habitat, size-specific predation, and density-dependent food competition (Smith, 1983).

With high primary productivity, food availability is likely to be high and although niche overlap can be high, tadpoles are most likely to be regulated by predators. Heavy predation (along with dessication of the pond) would select for rapid development, constraining the predator to breeding early in the spring (Wassersug, 1975). Also, inter- and intraspecific competition can cause growth inhibition, but predatory pressures may cause selection for

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rapid development and metamorphosis at small sizes in prey, and the predator would be selected for early breeding to exploit the influx of tadpoles in a pond (Wassersug, 1975).

On the contrary, by laying eggs singly throughout the summer, it is suggested that barking tree frogs (Hyla gratiosa) are dispersing young throughout space and time, and that disruptive coloration and rapid growth to a less vulnerable size may increase the survival of their tadpoles (Caldwell et. al, 1980). Anurans spend a short time in metamorphosis in order to minimize the time spent with a degenerating tail and underdeveloped legs, which are liabilities on both land and water (Wassersug and Sperry, 1977).

During the egg and larval periods, aquatic breeding anurans are exposed to many different types of vertebrate and invertebrate predators. As a response to predation, some animals have developed unpalatable or toxic secretions. Many adult anurans (Dendrobatidae, Bufonidae) are toxic. It is also known that some toad eggs are unpalatable (Licht, 1968), and that Bufo tadpoles are unpalatable to fish (Voris and Bacon, 1966; Kruse and Stone, 1984), and aquatic insects (Brodie et al. 1978; Formanowicz and Brodie, 1982).

Bufo larvae (black in color) presumably are conspicuous to visual predators and gregarious for thermoregulatory and anti-predatory purposes (Waldman and Adler, 1979). They are also highly density tolerant, have

an alarm reaction, and school in a polar manner (Wassersug, 1973). It is thought that schooling may be an anti-predatory behavior, because upon capture, an alarm pheremone is emmitted from the injured tadpole (Pfeiffer, 1966). Sibling recognition has been shown to occur, therefore kin selection is thought to be the mechanism behind tadpole schooling behavior (see Waldman and Adler, 1979).

Unlike bufonid eggs and tadpoles, Licht (1969) found that treefrog (hylid) egg masses were palatable to salamanders (Ambystoma gracile) and fish. Hyla crucifer tadpoles are also palatable and strongly preferred over Bufo spp. tadpoles by largemouth bass (Kruse and Stone, 1984), newts and salamanders (Walters, 1975), and the predatory insects Dytiscus and Lethocerus (Formanowicz and Brodie, 1982). Spring peeper tadpoles are a sandy brown color and move much less than Bufo tadpoles, making them a highly cryptic tadpole species (Kruse, unpublished data). They are not gregarious and when disturbed they tend to swim off very quickly for a short distance, then stop abruptly and settle to the pond or tank bottom. Morin (1981) found that in predator-free enclosures, Hyla crucifer tadpoles have a low survivorship relative to other tadpole species present (suggesting inferior competitive abilities), but in enclosures containing predatory newts, the species composition was reversed, suggesting that Hyla competes successfully with other tadpole species when a

predator is present, probably due to its cryptic behaviors.

Predaceous diving beetles (Dytiscus fasciventris) are relatively large invertebrates that have a life span of more than a year. Both the adults and larvae can overwinter, and the adults copulate in April (Pennak, 1978). In southern Ontario, the eggs are laid in aquatic vegetation in April, and hatch in 8-13 days. The larval period (three instars) lasts about 30 days, after which it pupates in the soil at the pond edge (James, 1969). The new generation of adults emerge in June and July (Young, 1967). Branucci (1980) found that the subfamily Dytiscinae (which includes the genus Dytiscus) is found most frequently in ponds and ditches rich in detritus and live vegetation. Also, the larvae of diving beetles tend to stay more within the vegetation than adults do (Needham and Williamson, 1907).

Dytiscus as a larva has two spiracles on the last abdominal segment, and the mandibles are sickle-shaped and have a grooved canal through which digestive juices are injected in order to pre-digest food (Pennak, 1978).

Dytiscids are voracious predators, and are of economic importance to fisheries (Petersen, 1960). They feed on Chironomus and Micronecta, two important food items of fish, and on the fingerlings themselves (Bisht and Das, 1979). A dytiscid has even been observed attacking and killing a young garter snake (Drummond and Wolfe, 1981). They are considered "sit-and-wait" predators, and Kruse

(1983) has shown that D. fasciventris is an optimal forager on American toad (Bufo americanus) tadpoles. Similarly, D. verticalis is an optimal forager on wood frog larvae (Rana sylvatica) and spring peeper larvae (Hyla crucifer) (Formanowicz, 1984).

The role of prey motion in the ability of an aquatic predator to detect prey is well known (Ware, 1973; Wright and O'Brien, 1982). It has previously been demonstrated that Bufo americanus tadpoles are more vulnerable to predaceous diving beetle larvae (Dytiscus fasciventris) than are Hyla crucifer tadpoles because Bufo moves substantially more than Hyla does (Kruse, unpublished data). Also, Cooke (1971) showed that tadpoles treated with DDT move significantly more than normal tadpoles and are much more vulnerable to newt predators for this reason.

Although many conclusions regarding the tactile and olfactory abilities of Dytiscus have been made, the visual acuity of Dytiscus has not been addressed. All past works have addressed only the olfactory component of dytiscid foraging strategies.

In many cases, an aquatic invertebrate predator with opposing mandibles can capture and consume a larger prey item than can a vertebrate predator that swallows its prey whole, as in odonates vs. salamanders (Caldwell et. al 1980) and dytiscids vs. newts and salamanders (Brodie and Formanowicz 1983). Neill (1968) states that Acilius semisulcatus (Dytiscidae) is highly size-specific in its

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predation on Bufo valiceps larvae, and the ability to capture and consume prey is known to depend on the relationship of the prey size (body width) to the mandible size of the beetle larva (Young, 1967). In odonates, especially Libellula, tadpole size is a very important variable, and an increase in tadpole size results in a decrease in predation rate, and density effects do not affect this relationship (Travis et. al, 1985b). Dytiscus verticalis exibits a prey size preference that is described as a correlation between it's body size and the preferred prey's body size (Brodie and Formanowicz 1983).

The Dytiscus-Bufo-Hyla system is good for studying how morphologic and behavioral variation in prey species may influence its predation vulnerability. This study is an analysis of the predator-prey relationship between larval predaceous diving beetles, Dytiscus fasciventris Say (Coleoptera: Dytiscidae) and two anuran tadpole species, Bufo americanus (Bufonidae) and Hyla crucifer (Hylidae). These three species are syntopic in ephemeral and semi-permenant ponds in east-central Illinois.

In this study, the following experiments were designed to ask specific questions about the dytiscid-tadpole predator-prey relationship:

1. Depth preference experiment: Does Bufo, Hyla, or Dytiscus prefer a certain depth? How much do these species overlap with respect to their spatial organization?

2. Tadpole vulnerability with depth experiment: Is there a depth where Bufo and Hyla larvae are more vulnerable to Dytiscus?

3. Substrate color preference experiment: Does Bufo, Hyla, or Dytiscus prefer a certain substrate color? If so, is a darker or a lighter colored substrate preferred?

4. Tadpole vulnerability with substrate color experiment: Can Dytiscus capture tadpoles more effectively on a light colored substrate or a dark colored substrate? Is the relative vulnerability of these two species similar on these two substrate colors?

5. Structure preference experiment: Does Dytiscus prefer an area that contains vertical structure?

6. Movement experiment: Kruse (unpublished data) has shown that Bufo tadpoles move 8-10 times more than do Hyla tadpoles. Does the presence of a beetle larva change the amount of movement in either species? If so, is this change enough to cause a decrease or increase in the vulnerability of that species? Also, does the presence of either species of tadpole cause a significant change in the amount of movement a beetle larva exhibits?

7. Field vulnerability experiment: Do results from field enclosures parallel results from laboratory experiments? Do effects of density on

vulnerability levels differ between _Bufo_ and _Hyla_?
The roles of tadpole motion, tadpole coloration, contrast between prey and background, water depth, and microhabitat structural organization are all discussed in relationship to their evolutionary implications in this predator-prey system.

MATERIALS AND METHODS

General

The predators used in all experiments were final
instar larvae of the predaceous diving beetle <u>Dytiscus</u>
<u>fasciventris</u> Say (Coleoptera: Dytiscidae). The mean volume
of 12 randomly picked larvae was 0.85 ml (s.d.= 0.12). All
beetle larvae were collected between 13 May, 1985 and 3
June, 1985 from a small ephemeral pond five km south of
Charleston (Coles County) in east-central Illinois. They
were kept in 4 liter plastic containers with 2-3 liters of
water, some gravel, and a few live segments of <u>Elodea</u> or
<u>Naiad</u>. Beetle larvae were fed three tadpoles each day
between 8 and 12 hours before they were to be used in an
experiment. The larvae were identified using taxonomic
keys (Hatch, 1928; Peterson, 1960; James, 1969; Watts,
1970; Pennak, 1978) and by letting eight pupate in the lab
following procedures in Formanowicz and Brodie (1981), and
later identifying the newly emerged adults.

The two anuran prey species used in this study were
tadpoles of the American toad, <u>Bufo</u> <u>americanus</u>, and the
spring peeper, <u>Hyla</u> <u>crucifer</u>. These tadpoles were all
collected between 13 May, 1985 and 6 June, 1985 in
ephemeral and semi-permanent ponds within 10 km of
Charleston, Il. They were maintained in 40 liter aquaria
by segregating them according to species and date of
capture, and feeding them canned spinach <u>ad</u> <u>libitum</u>.

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Tadpoles were identified (Altig, 1970) and the developmental stage of each tadpole was determined using Gosner 1960 (Appendix 2). All tadpoles used were between Gosner stages 27 and 45, corresponding to the time between rear limb bud emergence and premetamorphosis.

Laboratory experiments were performed between 14 May, 1985 and 7 June, 1985 during the same time each day (0600-2000) at room temperature (22-25 C).

In all experiments, tadpole size and stage, and beetle larva size was determined after each run in order to minimize stress to the animals. Volume was used as a measurement of size in all cases. Tadpole volume was determined by blot-drying all tadpoles from each run for approximately 15 seconds, placing them in a partially filled titration buret, and measuring the amount of water displaced. Dividing the displaced water volume by the number of tadpoles in the run gave an average value for tadpole size. Tadpoles were used only once, and then preserved in 10% formalin for later identification and staging. Beetle volumes were determined the same way, except they were done individually in a larger buret, and not all individuals were preserved.

An acclimation period was used for all animals in all experimental runs, and water temperature was recorded at this time. Tadpoles were acclimated for between 10 and 30 minutes, and beetle larvae were acclimated for between 10 and 20 minutes, depending on the experiment (see Appendix 1

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for a summary of experiments).

In experiments that included a beetle larva and tadpoles, acclimation was performed by placing tadpoles in the tank and placing a single beetle larva in a small cylindrical cage, made of window screening 5 cm in diameter, in the center of the tank or quadrat. At the start of the run, the cage was gently lifted out of the water to release the beetle larva. In studies using quadrats, animals were considered to be in the quadrat containing the most anterior portion of the head. The time of tadpole capture, and carcass release, were always noted for analyzing beetle larvae intercatch intervals and feeding durations.

Sampling with replacement was used in all laboratory experiments that included a predator. Five to ten "replacement tadpoles" of the same species, stage, and size were maintained during all experiments. After a tadpole was captured, a replacement tadpole was immediately placed in the same quadrat, and the carcass was removed from the tank as soon as the beetle released it.

In all experimental arenas, Red flint #30 gravel (dark brown in color) and/or White dolomite #30 gravel were used as substrate. Most tests were done both with and without structure present in the water column. When structure was used, it consisted of plastic replicas of Elodea and Ludwigia. In experiments not related to depth, five cm of water was used; this depth enables the beetle larva to

respire easily. Also, since tadpoles are known to exibit phototropic responses (Wassersug, 1973), lighting for all experiments consisted of only one 40 watt incandescent lamp situated at least one meter above the apparatus in a position that presumably would not influence tadpole activity.

EXPERIMENTS

1. DEPTH PREFERENCE EXPERIMENT

To test for depth preferences in predators and prey, a special depth tank was constructed from plate glass (Figure 1). It was 182.9 cm long, 30.5 cm wide, and 40.6 cm deep with a slanted bottom that had a slope of 0.14. The tank was filled so that some gravel in quadrat 1 was exposed to the atmosphere to represent shoreline and the deep end had a maximum depth of 25.4 cm of water. The tank was divided into six quadrats with equal surface areas of 930 cm^2. A thin layer of red flint gravel was present for every experiment except Hyla runs, in which white gravel was used because Hyla tadpoles closely approximated red flint in both color and size, and were too difficult for the investigator to observe. Two 40 watt lamps were placed one meter above quadrats 2 and 5 and were the only sources of light. In a separate set of experiments, artificial plants were added to the tank to test the effects of vertical structure presence on depth choice (Figure 2).

Beetles were tested for one hour, and data consisted

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of the time that a beetle larva crossed each quadrat line. This resulted in the total time (in beetle-minutes, or BM) a beetle larva spent in each of the six quadrats (60 BM for each run). Ten tadpoles were tested for one hour, and each minute, plus or minus five seconds, the number of tadpoles in each quadrat were counted and recorded, resulting in 60 observations of 10 tadpoles for each run. Each one hour run therefore contained 600 tadpole-minutes (TM). Runs with structure (artificial plants) present were performed in the same way.

To analyze the effects of predator presence on prey depth choice and effects of prey presence on predator depth choice, ten tadpoles and one beetle larva were put in the depth tank simultaneously. Tadpole and beetle positions were recorded each minute for one hour, resulting in 60 BM and 600 TM per run. The time and quadrat number of a capture or attempt at capture (a lunge with mandibles open) was noted for use in vulnerability with depth experiments. This experiment was performed both with and without structure present.

The Chi-square goodness of fit test (equal expected frequencies) was used to test for any deviations from random in the distribution of animals throughout the depth tank (alpha value = 0.05).

2. THE EFFECT OF DEPTH ON TADPOLE VULNERABILITY TO BEETLE LARVAE

The effect that depth has on the vulnerability of tadpoles to predation by beetle larvae was tested in the depth tank in two different ways. In the first method, the depth tank was used as described in depth preference tests (Figures 1 and 2) to determine if there is a specific depth at which beetle larvae will capture tadpoles most frequently. Ten tadpoles and one beetle larva were tested for one hour, recording positions each minute (resulting in 600 TM) for later analysis of depth preference with a predator present. The quadrat in which a capture, hit and miss, or attempt at capture (a lunge with mandibles opened) occurred was noted.

In the second method, the depth tank was divided into three equal (surface area) quadrats: shallow (1), medium (2), and deep (3), by tight fitting opaque glass dividers (Figure 3). Runs were performed with and without structure present: when structure was used it was placed in the positions shown in Figure 2. Five tadpoles of one species and one beetle larva were put in each quadrat and run for two hours. Mixed runs, consisting of three equal sized tadpoles of each species and one beetle larva were also performed.

The data for each run consisted of the number of tadpoles captured in each quadrat. These data were analyzed using the Chi-square goodness of fit test (equal expected frequencies, alpha level = 0.05).

3. SUBSTRATE COLOR PREFERENCE EXPERIMENT

To test for substrate color preference in beetle larvae and tadpoles, a one meter diameter plastic wading pool was set up with brown gravel and white gravel covering exactly half of the bottom, and five cm of water. Ten approximately equal size and stage tadpoles were tested for 30 minutes, and data consisted of counts of the tadpoles in each area each minute, resulting in 300 TM per run. Beetle runs lasted 30 minutes (30 BM): the time when a beetle larva crossed over the line between quadrats was recorded, resulting in the total time the beetle spent in each quadrat.

The Chi-square goodness of fit test (equal expected frequencies) with the Yates correction factor was used to determine if any significant deviations from random occurred in the distribution of animals on the different substrates (alpha value = 0.05). This experiment acted as a control for testing the vulnerability of tadpoles to beetle larvae on the two different colored substrates; the percentage of time spent in each area in this test was used in deriving Chi-square expected frequencies for the tadpole vulnerability with color experiment (see next section - Exp. 4).

4. THE EFFECT OF SUBSTRATE COLOR ON TADPOLE PREDATION VULNERABILITY TO BEETLE LARVAE

To test for predation vulnerability of tadpoles on

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different substrate colors, a 40 liter aquarium was divided in half (two equal sized quadrats), brown gravel was on one side and white gravel on the other (Figure 4). Backgrounds of brown cork and white paper were added to the outside of the tank to match the substrate colors and the water depth was set at five cm. Ten tadpoles and one beetle larva were placed in the tank and tested for one hour during which their positions were recorded each minute, resulting in 600 TM and 60 BM in each run. When a beetle caught a tadpole or lunged at one with mandibles opened, this event was noted with respect to the quadrat in which it occurred.

Data were again analyzed using the Chi-square goodness of fit test with the Yates correction factor (alpha value = 0.05). In this analysis, however, the expected tadpole vulnerability frequencies were derived from results of the tadpole color preference tests. First, the percent of time a tadpole species spent in each area (during color preference tests) was calculated. These percentages were then used in calculating the expected number of captures that should occur in each area if background color does not affect capture frequency (Table 4). This method of data tabulation compensates for any differences in capture frequency that result from a potential preference (of tadpoles) for a given substrate color.

5. STRUCTURE PREFERENCE EXPERIMENT

To test potential preferences for microhabitat spatial

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organization that may occur in _Dytiscus_, a 1 meter diameter
wading pool was set up with a brown substrate and five cm
of water. Live and artificial plants were placed on one
side of the pool so that exactly one half of the pool
contained structure and the other did not. Each run was
one hour long, in which the position of the beetle was
recorded each minute, resulting in 60 BM for each run.

A Chi-square goodness of fit test (equal expected
frequencies) with the Yates correction factor was used to
determine if beetle larvae prefer a structured or an
unstructured environment (alpha value = 0.05).

6. MOVEMENT EXPERIMENT

To test for the amount of beetle larvae movement with
and without prey present, and relative movement of the two
tadpole species with and without a predator present, a 40
liter aquarium was divided into eight equal size quadrats
(Figure 5). A thin layer of white gravel was added so the
quadrat boundaries could still be seen. Beetle larvae were
tested first so tadpole odors would not influence their
movement, and tank water was changed after each run in
which both predator and prey were present. Results of
Hrbacek (1950) and Pfeiffer (1966) show that an "alarm
substance" is emitted by injured _Bufo_ tadpoles, and that
this substance alters the behavior of conspecifics.

Beetles were tested for 15 minutes, and data consisted
of the number of quadrats the anterior portion of their

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head entered. When beetle larvae were run with tadpoles, data were of the same type, but capture times and carcass release times were also recorded so runs in which a beetle larva spent mostly eating could be differentiated from runs in which a beetle larva captured no tadpoles.

Tadpoles were run in groups of 10 for 15 minutes. One tadpole in each run was randomly chosen and followed for the entire time period, recording the number of quadrats its body entered with a hand-counter. If more than one tadpole occurred in the randomly chosen quadrat, a coin was flipped to choose a tadpole randomly from that quadrat.

In tests with both predator and prey present, it is possible for the selected tadpole to be captured and eaten. In these cases, the clock was stopped and a replacement tadpole of equal stage and size was put in the tank. Another tadpole (possibly the replaced one) was then randomly chosen and followed for the remainder of the 15 minute run. The time of capture and carcass release was also recorded.

Analyses of tadpole data were performed in three different ways. First, differences between Bufo and Hyla movement were analyzed using an independent t-test (alpha level = 0.05, 2-tailed). Then, differences in tadpole movement (both species) with and without a predator present were also analyzed, using the same test and alpha value. Finally, the differences in movement between early and late stage tadpoles (Bufo only) were analyzed with a one-way

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ANOVA test (alpha level = 0.05).

The beetle movement data were analyzed with the Kruskal-Wallis test (alpha level = 0.05) to determine if there was a difference in beetle larvae movement with and without tadpoles present.

7. TADPOLE VULNERABILITY IN FIELD ENCLOSURES

In order to expose predators to prey in more natural conditions, animals were placed in field enclosures and checked every 24 hours. The enclosures were made of 2.5 x 5.0 cm lumber framing with window screening on the inside of the frame (Figure 6). Having the frame entirely on the outside of the cage walls eliminates any unnatural cover that tadpoles would have if the frame were on the inside. Window screening keeps even small aquatic organisms out, but allows algae to enter for the tadpoles to eat. These enclosures were placed in a pond south of Charleston Il. a few days prior to experimentation so that algae could establish. Three one-meter willow (Salix sp.) branches and a 5 cm diameter log approximately 0.5 meter long were placed in each of the enclosures for all of the experiments.

Tadpoles were placed in the enclosures at single species densities of 50 and 20 per enclosure and mixed species densities of 20 Bufo and 20 Hyla per enclosure. Twenty-four hours later, the tadpoles were taken back to the lab, where they were counted, sized, and preserved.

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Beetle larvae were used only once in field experiments.

An analysis of the field data was performed using the Chi-square goodness of fit test (equal expected frequencies) with the Yates correction factor (alpha level = 0.05).

GENERAL

Predaceous diving beetle larvae (Dytiscus fasciventris), American toad tadpoles (Bufo americanus), and spring peeper tadpoles (Hyla crucifer) were found to occur syntopically in ephemeral ponds in east-central Illinois (Coles County), and beetle larvae are known to be important predators on these tadpole species (Kruse, 1983).

A total of 1096 tadpoles (676 in the laboratory; 420 in the field study) and 49 beetle larvae were used in the study. Of the 620 tadpoles (310 Bufo; 310 Hyla) exposed to predators in the laboratory, 101 were captured and eaten. Bufo was captured significantly more (67 captures) than was Hyla (34 captures) in a combined analysis of all laboratory experiments that included predators and prey (X^2 = 8.92; 1 d.f., P << 0.05).

The amount of time beetle larvae spent feeding was analyzed only for the 66 captures in which the beetle larva finished eating the prey item before the run was completed. Beetle larvae spent an average of 30.6 minutes (s.d.= 14.6; range 9-80 minutes) eating tadpoles that had a mean size of 0.12 ml (s.d.= 0.025).

The intercatch intervals (the time between when a tadpole is discarded and another one is captured, or from the begining of the run to the first capture) were analyzed to test for differences between the amount of time it takes

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beetle larvae to capture the two tadpole species. Beetle
larvae captured Bufo tadpoles (n=67) in an average of 11
minutes (s.d.= 8.53), and Hyla tadpoles in an average of 22
minutes (s.d.= 19.47). These results are significantly
different when tested with the Mann-Whitney U test (Z =
2.32; P = 0.020; 2-tailed), suggesting that Bufo are
captured significantly faster by beetle larvae than are
Hyla.

1. DEPTH PREFERENCE

In laboratory studies, both Bufo and Hyla tadpoles
of similar stages (Appendix 2) significantly preferred the
deep end of the depth tank (P << 0.05) whether a predator
was present or not (Table 1). The presence of structure
did not affect the distribution of tadpoles in the depth
tank (data not shown).

In six one-hour runs, beetle larvae significantly
preferred the shallow end of the depth tank (0.0 - 4 cm
deep) when tadpoles were absent (Table 2). In 11 runs with
tadpoles present, Dytiscus occurred significantly more
(P < 0.05) in depths ranging from 4.3 cm to 17.1 cm deep.
When beetle foraging times are analyzed separately from
feeding times during 11 runs with tadpoles present, the
bias of a depth choice while eating is removed. While not
eating, Dytiscus was again found in the middle quadrats 2,
3, and 4 significantly more (P << 0.05) than in other
quadrats. While eating Bufo, Dytiscus was found

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significantly more (P << 0.05) in quadrats one and two or floating at the surface. Although Dytiscus ate Hyla exclusively (P << 0.05) in two deep quadrats, it was always at a location in aquatic vegetation at the water surface (Table 2). After all eight captures in this experiment, the beetles immediately moved with the captured tadpole to a quadrat shallower than the one in which the capture occurred.

2. VULNERABILITY WITH DEPTH

Results from 10 two-hour runs suggest that tadpoles were slightly more vulnerable to beetle larvae in shallow water than in deep water, however, these results are not statistically significant to the 0.05 level for Bufo (P > 0.05), Hyla (P > 0.05), or for both species analyzed together (P < 0.10) (Table 3).

Tadpole vulnerability with depth was also summarized for depth preference experiments with predators present. Tadpoles of both species were caught slightly more in the deep half of the tank where they tended to aggregate (data not shown). Six tadpoles were caught in the three deep quadrats, and two were caught in the three shallow quadrats. Of the eight tadpoles caught, six were Bufo and two were Hyla. These data were not statistically analyzed.

3. SUBSTRATE COLOR PREFERENCE

During six experimental runs of 30-minutes each, Hyla

showed no significant preference for a particular substrate color ($P > 0.05$), whereas Bufo did significantly prefer being in the white area ($P < 0.05$) (Table 4). Dytiscus significantly preferred the area with brown substrate color ($P < 0.05$) during eight 30-minute runs.

4. VULNERABILITY WITH COLOR

In a combined analysis, both tadpole species were significantly more vulnerable to predators ($P \ll 0.05$) in the area with white substrate and background than in the darker area (Table 5). Hyla tadpoles appear to have a higher relative vulnerability on the white area than do Bufo larvae. A correction in Chi-square expected frequencies for Bufo was made because they spent significantly more time in the white area during substrate color preference tests. Despite this, toad larvae are still captured significantly more frequently ($P \ll 0.05$) in the white area. The greater total vulnerability of spring peeper tadpoles in this experiment might be attributed to the larger number of runs performed with this species (Appendix 1).

5. STRUCTURE PREFERENCE

During three runs of one hour each (180 BM), Dytiscus spent significantly more time (134 BM) in the quadrat with vertical structure present than it did in the one without structure ($P \ll 0.05$). Also, during depth preference

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experiments with structure, Dytiscus spent a greater percent of time on plants when it was in deeper quadrats, and spent more time feeding in plants at the surface, than it did feeding on the bottom (Table 2).

6. MOVEMENT

In general, Bufo tadpoles moved significantly more than Hyla tadpoles of equal developmental stages (t= 4.25; d.f.=13 P < 0.05; 2-tailed test) (a vs. c - Table 6). Also, earlier developmental stages of Bufo moved significantly more than did late stages (F= 11.85; P << 0.05) (a - Table 6). The presence of a beetle larva did not appear to affect the amount of movement Bufo tadpoles exhibit (t= 1.29; d.f.=13, P > 0.05), nor does it effect the amount of movement Hyla tadpoles exhibited (t= 0.82; d.f.= 13, P >> 0.05) (b and d - Table 6).

Results from beetle movement experiments suggest that beetle larvae moved slightly less when tadpoles were present in the arena, even when the runs in which a beetle was eating a tadpole are excluded (Table 7). These results are not significant, however, using the Kruskal-Wallis test (H = 2.93; d.f.= 2, P > 0.05).

FIELD VULNERABILITY

As expected, more tadpoles of both species were killed in the enclosures containing higher tadpole densities. No significant difference occurred (P > 0.05) between the

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vulnerabilities of the two species in this experiment at either density, however (Table 8). The toad tadpoles were, however, at a later stage of development than were the spring peeper tadpoles (Appendix 2), and the relative movements of the two species were presumed to be approximately equal.

DISCUSSION

DEPTH PREFERENCE

It is known that tadpole developmental time is a function of temperature, and that the relationship is a positive one, ie. the higher the temperature, the faster the development (Wilbur and Collins, 1973). For this reason, tadpoles should generally occur more frequently in warmer areas of a pond in order to speed development during this highly vulnerable period in their life cycle. Bufo is known to aggregate in kin groups and it has been found that water temperatures within these groups are significantly higher than temperatures in the surrounding water (Wassersug, 1973). From this information, it appears that tadpoles should prefer to aggregate in shallow water. My data suggest that Bufo tadpoles do not prefer shallow water, and that tadpoles do not utilize vertical structure preferentially. The reasons for these results are not entirely clear. Contrary to what is found in nature, in the depth tank, temperature differences between shallow and deep water were non-existent in any experiment, which might be a partial explanation for these results. Both species should act optimally when choosing between fast development (higher temperatures) and predator avoidance (deeper water or more cover). In the depth tank, they may have been able to sense the lack of temperature differential and were behaviorally attracted to deeper water to optimize predator

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avoidance (the volume would increase, therefore decreasing tadpole density). It is also possible that anuran larvae ended up at the bottom of the gradient in their random search for warm water (anecdotal observations indicated that tadpoles were primarily negatively buoyant, and needed to swim to maintain their position).

Beetle larvae have two caudal spiracles through which they must renew their air supply every few minutes (Pennak, 1978), and it appeared that they used them in buoyancy compensation as well as respiration. They could be positively or negatively buoyant by varying the amount of air they take in with their two caudal spiracles. Beetle larvae sometimes stayed at the surface for long periods, but upon decent they expelled some air (which should decrease diving time) or tried to counteract positive buoyancy by constantly swimming downwards until an underwater structure was grasped (which uses more oxygen and should decrease dive time). In a sit-wait predator, the act of returning to the surface for air can be viewed as a risk (Cook and Streams, 1984) that Dytiscus should tend to minimize, since it directly interferes with this foraging strategy. Also, it may be exposing itself to larger visual or tactile oriented predators such as ranid frogs, or fishing spiders of the genus Dolomedes, both of which were found in the study area. By remaining in shallow water or on a plant near the surface, where the beetle larva can be affixed to the substrate and able to

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respire and remain motionless, costs of foraging should be minimized. Results of experiments with and without prey present indicate that Dytiscus does prefer to forage, and to eat, in shallow water (or in plants at the water surface). These results also suggest that the presence of tadpoles as prey items does affect the behavior of Dytiscus with respect to the depth at which it prefers to forage.

VULNERABILITY WITH DEPTH

Anecdotal observations during depth preference experiments with beetle predators present suggest that tadpole captures occur slightly more frequently in the deep end of the tank. This may have been due to the significantly increased presence of tadpoles in that area of the tank. Consequently the depth tank was separated physically into three distinct quadrats for further vulnerability experiments.

The results of these tests, though not statistically significant, indicate that beetle larvae are able to capture tadpoles slightly better in shallow areas. Combined with the decreased costs of staying in shallow water is the increased chance that a tadpole will have to swim directly past a waiting beetle, not above or below it. For these reasons, it seems logical to assume that beetle larvae may be more efficient predators on tadpoles in shallow water. The effects of using white gravel during the Hyla runs is not known, but this procedure may have

overestimated true Hyla vulnerability. More experiments need to be designed to further test aspects of tadpole vulnerability to Dytiscus over a range of depths.

SUBSTRATE COLOR PREFERENCE

This experiment was designed as a control for further vulnerability tests, but the results are interesting. The preference for the white area by Bufo tadpoles may be explained by theories of aposematism. Bufo are distasteful to vertebrate predators (Brodie et al. 1978) and to predators that must come in contact with the skin of this tadpole species. It is also jet black, swims almost constantly, and tends to aggregate with siblings in a manner consistent with kin selection theory (Wassersug, 1973). These characteristics make Bufo tadpoles a highly conspicuous animal, and theories of aposematism do not neccessarily contradict the idea that Bufo tadpoles are black to derive a thermal advantage. If kin selection is operating on tadpoles, the learning experiences of predators are of great importance to the fitness of each individual in an aggregate, and any tadpole behavior that can enhance that learning experience should be selected for over evolutionary time. One way to enhance the learning experience may be to increase the contrast between prey and background (Cook and Streams, 1984). Bufo could do this if it is able to differentiate between high and low contrast areas. My data suggest that Bufo is assessing background

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color; however, this study does not concentrate on the mechanisms that are involved in this possible ability to differentiate substrate colors.

As a predator on Bufo larvae, Dytiscus is at an extreme advantage over animals that swallow tadpoles whole. By piercing through the skin, it is avoiding the primary anti-predatory defense that Bufo tadpoles have. It is very likely that bufonids have evolved toxins in their skin as an anti-predator mechanism against engulfing-type predators (e.g. fish and salamanders), suggesting that predaceous beetle larvae are the primary predators on toad larvae. It is at best only speculation that the evolution of dytiscid mouthparts was in part dictated by the need to pierce through toxic tadpole skin. Larval dytiscid mouthparts are probably primarily adapted to pierce through arthropod exoskeleton and, as a result, could be well pre-adapted for avoiding Bufo skin secretions. It is also ingesting less of each prey item than a swallowing predator would (if it could handle the toxin) and must be able to capture a relatively greater number of prey items than a comparable sized swallowing predator per unit of time. Because of these advantages, Dytiscus larvae are very effective predators on Bufo tadpoles where these species are syntopic.

The random distribution of Hyla tadpoles on the two backgrounds might be explained in terms of cryptic behaviors. Hyla is crypticly colored and palatable to

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vertebrate predators that swallow their prey (Formanowicz and Brodie 1982). Natural selection theory predicts that cryptic animals should have an ability to select substrates with which to blend. Hyla, in this experiment, did not prefer the area that would give it the most protection. It is known that Hyla crucifer tadpoles move very little (Kruse, unpublished data) which may be considered a cryptic behavior. Remaining motionless on a substrate may therefore have been more important in the evolution of Hyla crucifer behavior than was background matching.

Predaceous diving beetle larvae need to remain concealed from their own predators, and since these are probably largely sit-and-wait predators, they must remain concealed from their own prey. The fitness of a beetle larva would be enhanced if it were able to detect a suitable background and remain relatively motionless upon it. The results of this experiment indicate that Dytiscus is able to choose a substrate that it can blend with. Again, the proximate mechanisms have yet to be discovered (it is likely visual) by which Dytiscus chooses a specific substrate color.

TADPOLE VULNERABILITY WITH SUBSTRATE COLOR

Results of this experiment shed some light on the previous section. In past studies, Dytiscus has been referred to as a largely olfactory predator (Formanowicz, 1984). This is suggested here by beetle larvae movement

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experiments, in which beetles move slightly (but not significantly) less during runs in which tadpoles are present (see tadpole movement section). This would be expected in a sit-wait predator; when prey are absent, it should actively search more than when prey (or the scents of prey) are present (Formanowicz, 1984). The visual acuity of this species has been overlooked in past studies, however. Dytiscus larvae have six pairs of ocelli located laterally and posterior to the mandibles (Pennak, 1978), but the extent of their visual field is not known.

Results herein indicate that Dytiscus has the ability to use vision to capture tadpoles. Firstly, during experiments of vulnerability with depth in the partitioned depth tank, both tactile and olfactory cues were controlled because the tadpoles were on the other side of a glass plate. Anecdotal observations suggest that beetle larvae interacted (or tried to) with the tadpoles on the other side of the glass. The tracking ability of the beetle larvae appeared to be quite good, and the strikes at each tadpole (through the glass) were accurate. After this was observed, the glass was taped in order to block the beetle's view into the next quadrat.

Secondly, no significant differences should occur between the brown area and the white area in the interactions of beetle larvae and tadpoles if these animals are not using visual cues to capture prey. If they are able to use vision in capturing prey, there should be a

significant increase in the number of interactions with tadpoles in an area where the contrast between prey and substrate is high (Cook and Streams, 1984). Thirdly, Hyla did exhibit a much higher difference between vulnerability on the two areas than did Bufo, because the former are almost invisible on the brown area, wheras Bufo can be seen well on both substrate colors. Clearly, in a pond with low visibility, Dytiscus would rely on chemical/ tactile cues to locate an area where prey occur, then tactile information when actually capturing prey. In a pond that has clear water, Dytiscus might be able to use chemical cues first, and then a combination of visual and tactile information when making the capture. This conjecture is largely congruent with the results of Vinyard and O'Brien (1976), who found that turbidity in a pond decreases the visual reactive distance of fish predators, causing them to use a tactile detection method (the lateral line). The pond from which these animals were collected has quite clear water from the time ice clears until mid-summer, suggesting that Dytiscus may be using vision to capture prey in it's natural environment.

MOVEMENT EXPERIMENTS

In a previous study, Bufo americanus tadpoles were found to move eight to twelve times more than Hyla crucifer tadpoles (Kruse, unpublished) of equal developmental stage. This was determined to be the major reason why Bufo are

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more vulnerable to beetle larvae than are Hyla. The amount
of movement observed in Hyla is approximately equal to the
amount of movement observed in late developmental stage
Bufo tadpoles. Hyla appears to move very little at all
developmental stages, but this was only an anecdotal
observation and cannot be statistically tested from data in
this study. Also, Hyla tadpoles are larger than equal-
staged Bufo tadpoles and have a relatively longer tail.
When disturbed, Hyla tadpoles dart away at high speed, then
rapidly stop swimming and sink to the bottom, where they
remain motionless until disturbed again. In contrast, Bufo
tadpoles appear to be in almost constant motion, which
should increase its relative vulnerability substantially.
These results are similar to those of Wright and O'Brien
(1982), who found that prey motion more than doubled the
distance at which midge fly larvae (Chaoborus) could be
located by white crappie predators.

Results of this study show a decrease of movement in
Bufo tadpoles as development proceeds. A logical
explanation is that limb development tends to increase the
drag on a swimming tadpole. This, coupled with the loss of
tail mass makes swimming increasingly difficult, and the
tadpole must necessarily slow down. In contrast, Hyla
appears to move very little irrespective of developmental
stage (anecdotal observations). These findings indicate
that the vulnerability of Bufo to beetle larvae may change
(decrease) over time, and that Hyla vulnerability may not.

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It is therefore logical to assume that early in the tadpole stage *Bufo* tadpoles are much more vulnerable to beetle larvae than are *Hyla* tadpoles, and that later in tadpole development (premetamorphosis) the two species have similar vulnerabilities. A question that this study does not address is "do *Bufo* tadpoles move away from the alarm substance, or do they just generally move more?" A controlled experiment is needed in which a group of tadpoles are exposed to tadpole skin extract in an arena designed to reveal relative movement and tadpole locations at given points in time.

Beetle larvae may (although results are not significant) tend to move more when in a tank with freshwater and no tadpoles than they should with tadpoles present (i.e., they can assess tadpole density), which is consistent with theories of optimal foraging in a sit-wait predator (Kruse, 1983). If a sit-wait predator encounters no prey, it may be beneficial to give up concealment from predators and go out foraging until it finds an area with prey (assuming prey distribution is patchy). If this is true, beetle larvae should move more in the presence of *Hyla* than *Bufo*. That *Dytiscus* moved slightly (but not significantly) more with *Bufo* present than it did in the presence of *Hyla* is possibly explained by looking at the tadpole stages. In this experiment, *Hyla* stages are early, and *Bufo* stages are late (Appendix 2), making their relative movements somewhat equal, and the differences may

then be due to random variations in runs. Clearly, more experiments need to be designed to test these hypotheses further.

FIELD VULNERABILITY

This experiment was originally designed to reveal specific tadpole density effects in this predator-prey relationship. However, the only density effect observed was that beetles were able to capture and eat more tadpoles in a 24 hour period in the enclosure with higher tadpole density.

Differential vulnerability results in the field are much more interesting, and relate to tadpole movement experiments. Bufo and Hyla were equally vulnerable in this experiment, but Bufo tadpoles were well advanced in their larval development (Appendix 2), indicating that their relative movement was very similar to that of Hyla. If differential vulnerability in these tadpole species was due to factors other than the amount of movement they exhibited, this experiment should have revealed those factors by showing a difference in the two species' vulnerability. There was no difference, further suggesting that tadpole movement maybe an important determinant of tadpole vulnerability to aquatic beetle larvae. Another factor that may have been important in these results was the high turbidity of the water in the test pond. The turbid water would have decreased the reactive distance of

<u>Dytiscus</u> substantially, possibly forcing it to use non-
visual methods of prey location.

SUMMARY

In conclusion, it has been shown in this study that
<u>Bufo</u> <u>americanus</u> tadpoles are generally more vulnerable to
predaceous diving beetle larvae than are <u>Hyla</u> <u>crucifer</u>
tadpoles, and that this is related to the amount of
movement tadpoles exhibit. The roles of tadpole movement,
microhabitat utilization, and species composition of a pond
over time are important in the evolution of anuran-dytiscid
predator-prey interactions and deserve further study.

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Table 1. The number of tadpole minutes spent in each quadrat during depth preference experiments. Chi-square expected values are in parentheses.

			Quadrat					
	(shallow)				(deep)			Chi-
Species	1	2	3	4	5	6	Total	square
Bufo	769	932	941	676	783	1299	5400	269.9*
n=90	(900)	(900)	(900)	(900)	(900)	(900)		
Bufo w/beetle	358	322	587	690	586	1657	4200	1716.5*
n=70	(700)	(700)	(700)	(700)	(700)	(700)		
Hyla	81	107	199	251	442	1320	2400	2745.9*
n=40	(400)	(400)	(400)	(400)	(400)	(400)		
Hyla w/beetle	112	123	190	245	239	1491	2400	3610.0*
n=40	(400)	(400)	(400)	(400)	(400)	(400)		

* $P \ll .05$ in all.

Table 2. The number of beetle minutes spent in each quadrat of the depth tank during depth preference experiments. Chi-square expected values are in parentheses.

		Quadrat						
	(shallow)			(deep)				
Species	1	2	3	4	5	6	Total	Chi-square
Dytiscus alone n=6	248 (60)	78 (60)	27 (60)	4 (60)	1 (60)	2 (60)	360	778.9
Dytiscus w/Bufo n=7	76 (70)	94 (70)	40 (70)	93 (70)	44 (70)	73 (70)	420	38.9
Dytiscus w/Hyla n=4	27 (40)	29 (40)	75 (40)	52 (40)	56 (40)	1 (40)	240	85.9
Dytiscus w/both n=11	103 (110)	123 (110)	115 (110)	145 (110)	100 (110)	74 (110)	660	26.1
Total Dytiscus not eating n=11	51 (81)	103 (81)	100 (81)	115 (81)	60 (81)	57 (81)	486	48.4
Dytiscus eating Bufo n=6	52 (22.3)	21 (22.3)	15 (22.3)	18 (22.3)	11 (22.3)	17 (22.3)	134	49.8
Dytiscus eating Hyla n=2	0 (6.6)	0 (6.6)	0 (6.6)	11 * (6.6)	29 * (6.6)	0 (6.6)	40	105.3

* Beetle was in structure at surface 100 % of the time
P < .05 in all

Table 3. Frequency of tadpole captures by beetle larvae in each quadrat during vulnerability with depth experiments.

| | Quadrat | | | | |
| | (shallow) | | (deep) | | Chi- |
Species	1	2	3	Total	square
Bufo	21	12	11	44	4.1*
Hyla	9	5	6	20	1.3*
Total	30	17	17	64	5.3+

* N.S. (P >.05)　　　+ N.S. (P < .10)

50

Table 4. The number of tadpole minutes spent in areas with brown and white gravel during substrate color preference experiments. Chi-square expected values are in parentheses.

| | Substrate Color | | | |
| | Brown | White | | |
Species	Brown	White	Total	Chi-square
Bufo	829	971	1800	11.20*
n=60	(900)	(900)		
Hyla	909	891	1800	0.18+
n=60	(900)	(900)		
Dytiscus	136	104	240	4.00*
n=8	(120)	(120)		

* P < .05   + N.S. (P > .05)

Table 5. The number of interactions between beetle larvae
and tadpoles in areas with brown background and white
background during vulnerability with color experiments.
Chi-square expected frequencies are shown in parentheses.
Unequal expected frequencies for Bufo were derived from
color preference experiments (see methods for explanation).

| Species | Substrate Color | | Total | Chi-square |
	Brown	White		
Bufo	7	30	37	7.32*
n=30	(17)	(20)		
Hyla	11	39	50	14.58*
n=60	(25)	(25)		
Total	18	69	87	26.84*
	(42)	(45)		

* $P \ll .05$

52

Table 6. Bufo and Hyla tadpole movement with and without Dytiscus present.

Species	Mean Volume (ml)	Median Stage	Stage Range	Mean Quadrats /minute	s.d.
a. Bufo	0.07	33	31-35	6.03	1.80
	0.17	38	36-39	3.88	2.69
	0.10	42	41-44	0.31	0.23
b. Bufo + Dytiscus	0.13	41	34-44	1.35	1.76
c. Hyla	0.25	35	33-38	0.38	0.15
d. Hyla + Dytiscus	0.15	35	30-37	0.46	0.24

Table 7. Beetle larvae movement with and without tadpoles
present, shown as quadrats per minute.

| | Tadpoles present | |
Tadpoles absent	Bufo a	Hyla b
2.07	0.33 *	0.73 *
0.27	0.73	0.07
0.80	2.60	0.73
3.40	0.73	0.13
2.40	0.47	0.87
$\overline{x}$ = 1.79	$\overline{x}$ = 0.97	$\overline{x}$ = 0.51
s.d.= 1.26	s.d.= 0.93	s.d.= 0.38

* = runs in which a beetle was eating a tadpole

a = Bufo median stage 40.5, range 34-44

b = Hyla median stage 35, range 31-38

Table 8. The number of tadpoles predated in 24-hour field enclosure experiments. The chi-square expected frequencies are in parentheses.

| | Density | | |
Species	20	50	Total
Bufo n=210	7	45	52
Hyla n=210	9	34	43
Total n=420	16	79	95
Chi-square	0.06 * (8)	1.27 * (39.5)	0.67 * (47.5)

* P > 0.05 (N.S.)

Figure 1. The depth tank apparatus used for depth preference experiments without structure.

DEPTH TANK

SLOPE = 0.14

30.5 CM

30.5 CM

|← 182.9 CM →|

| 1 | 2 | 3 | 4 | 5 | 6 |

WATER LEVEL

25.4 CM
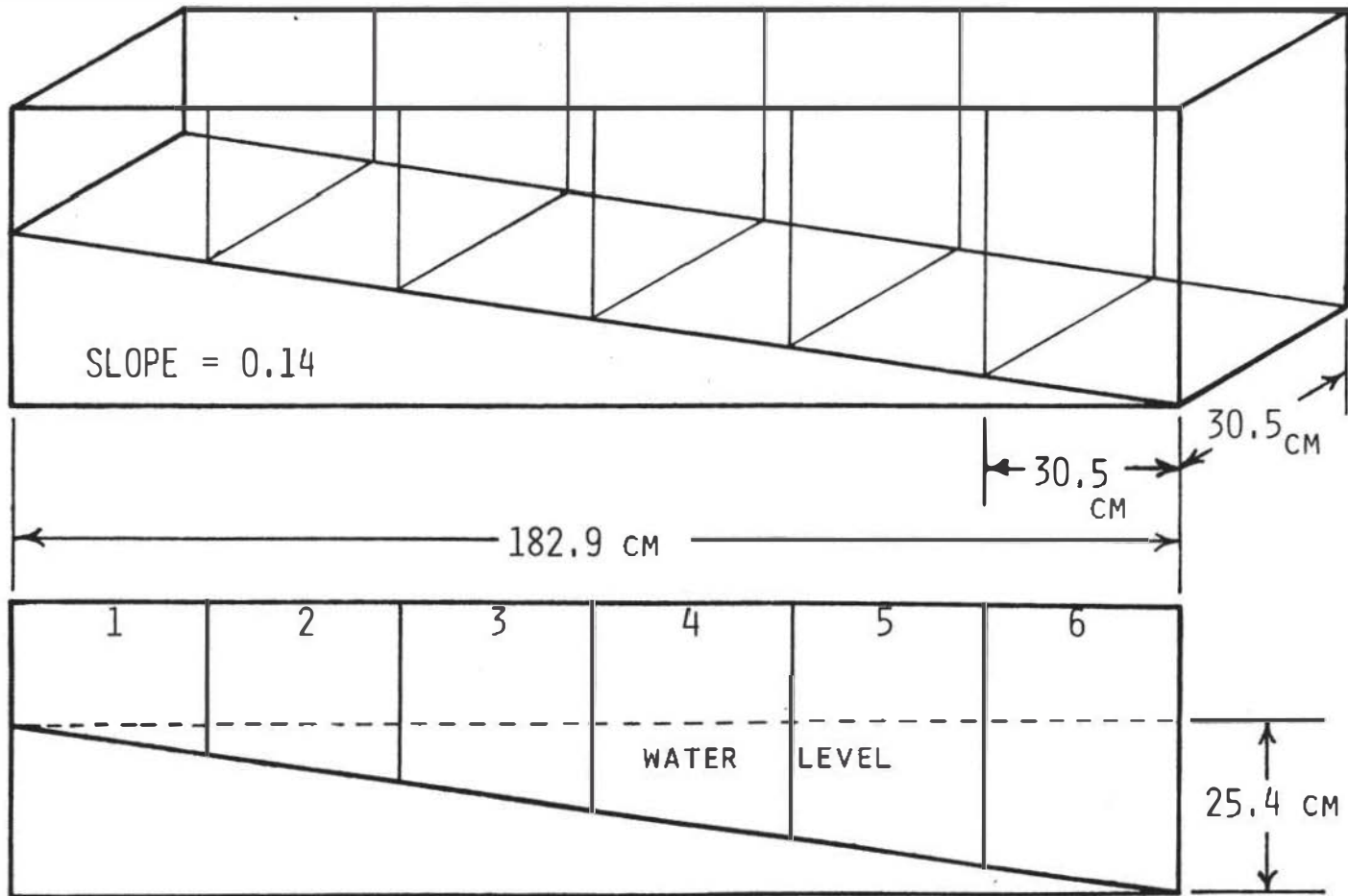
Figure 2. The depth tank set up for depth preference experiments with structure present. All dimensions are the same as in Figure 1. Fishing weights were clamped to the base of the plants to keep them in place. Four plants were placed in each quadrat in positions designated with an "x".

DEPTH TANK
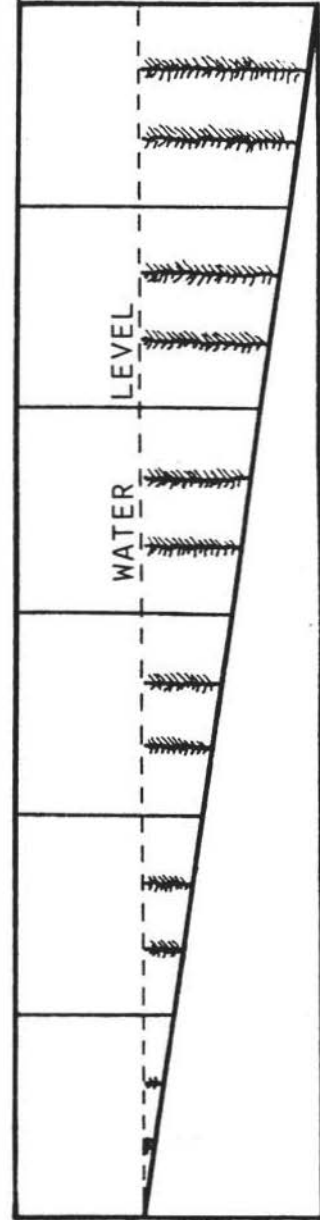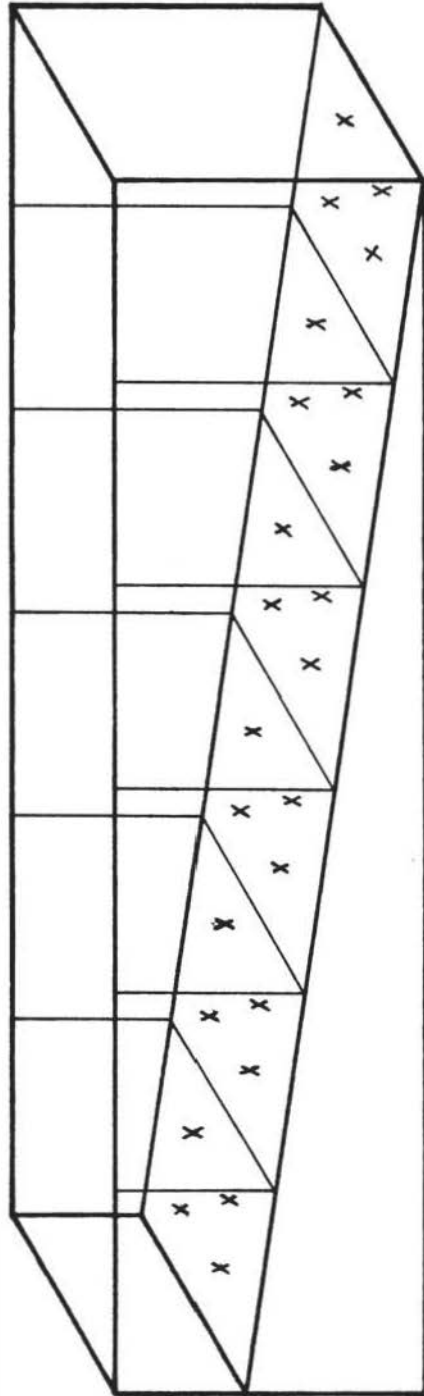
Figure 3. The depth tank, modified for tadpole vulnerability experiments in which the tadpoles and beetle larvae are confined to one specific depth range.

DEPTH TANK

PARTITION

30.5 CM

61 CM

1 2 3
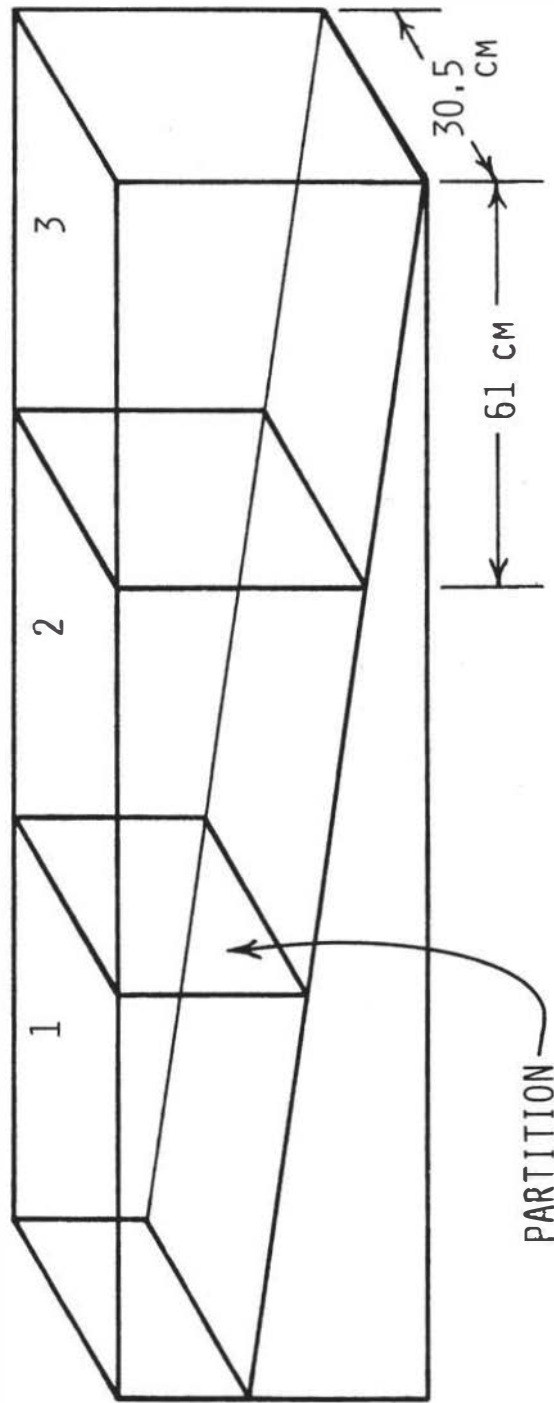
Figure 4. The 40 liter (10 gal.) tank used in the tadpole vulnerability with substrate color experiment.

TWO COLOR
SUBSTRATE TANK

5 CM

25.4 CM

25.4 CM

WHITE

BROWN

50.8 CM
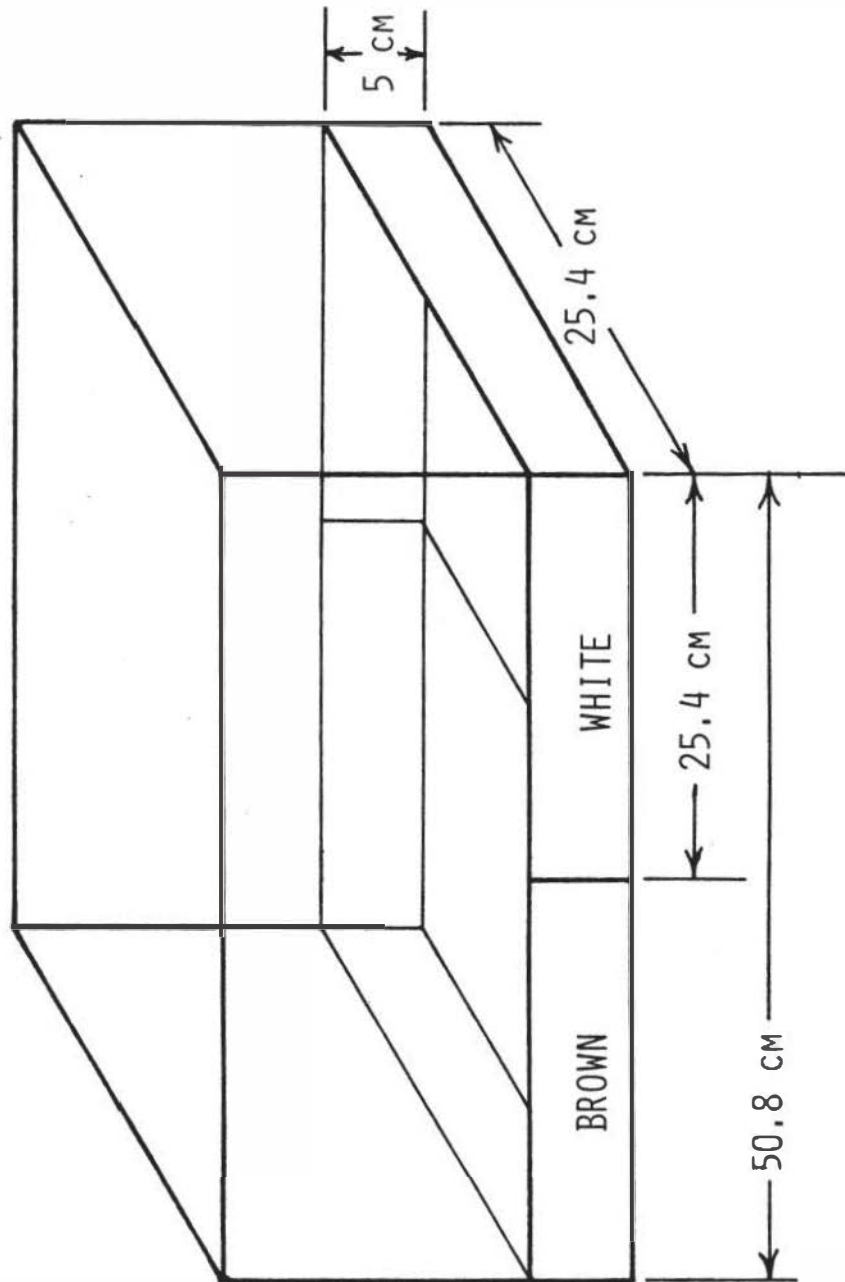
Figure 5. The 40 liter tank designed for movement experiments. Each of the eight quadrats have a surface area of 161.3 cm^2.

MOVEMENT
TANK

12.7
CM

12.7
CM

12.5
CM

50.8 CM
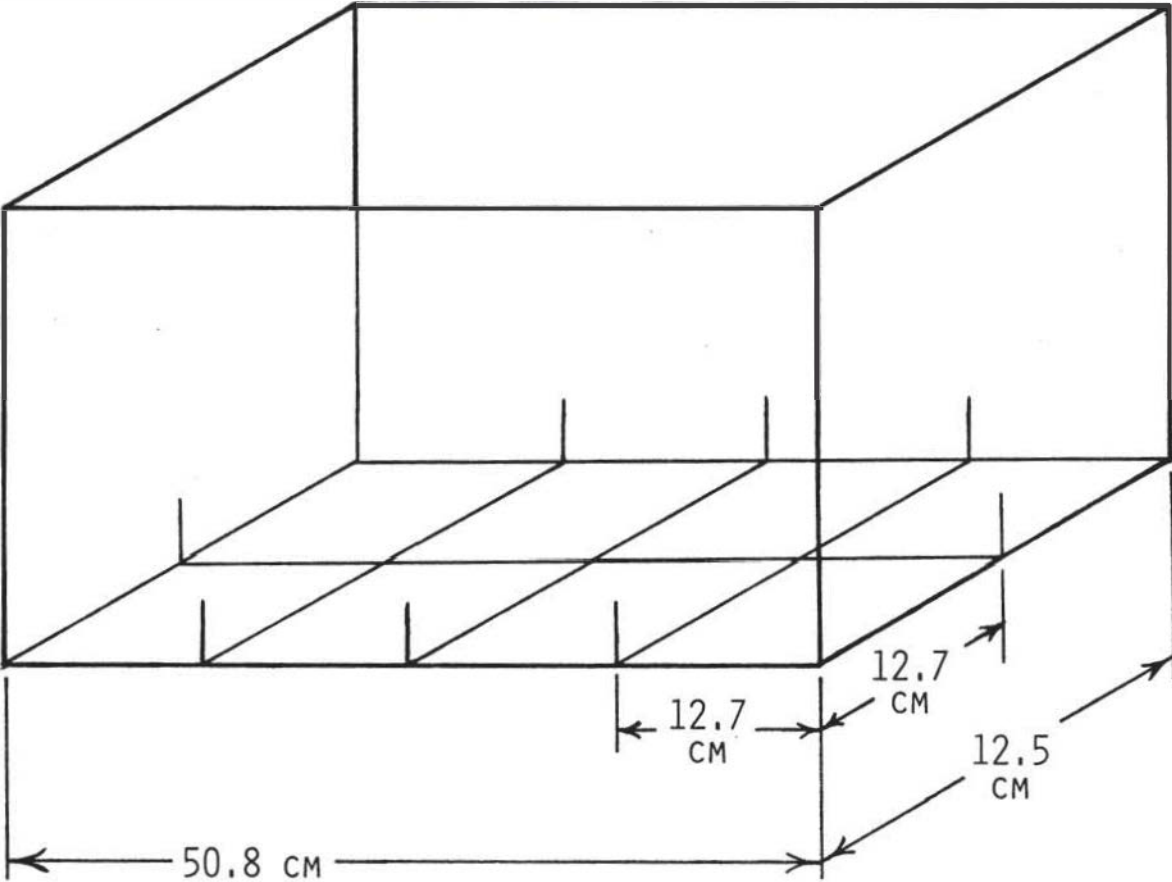
Figure 6. The field enclosure designed for vulnerability experiments.

FIELD ENCLOSURE

45.7 CM

91.4 CM

91.4 CM

WINDOW SCREENING
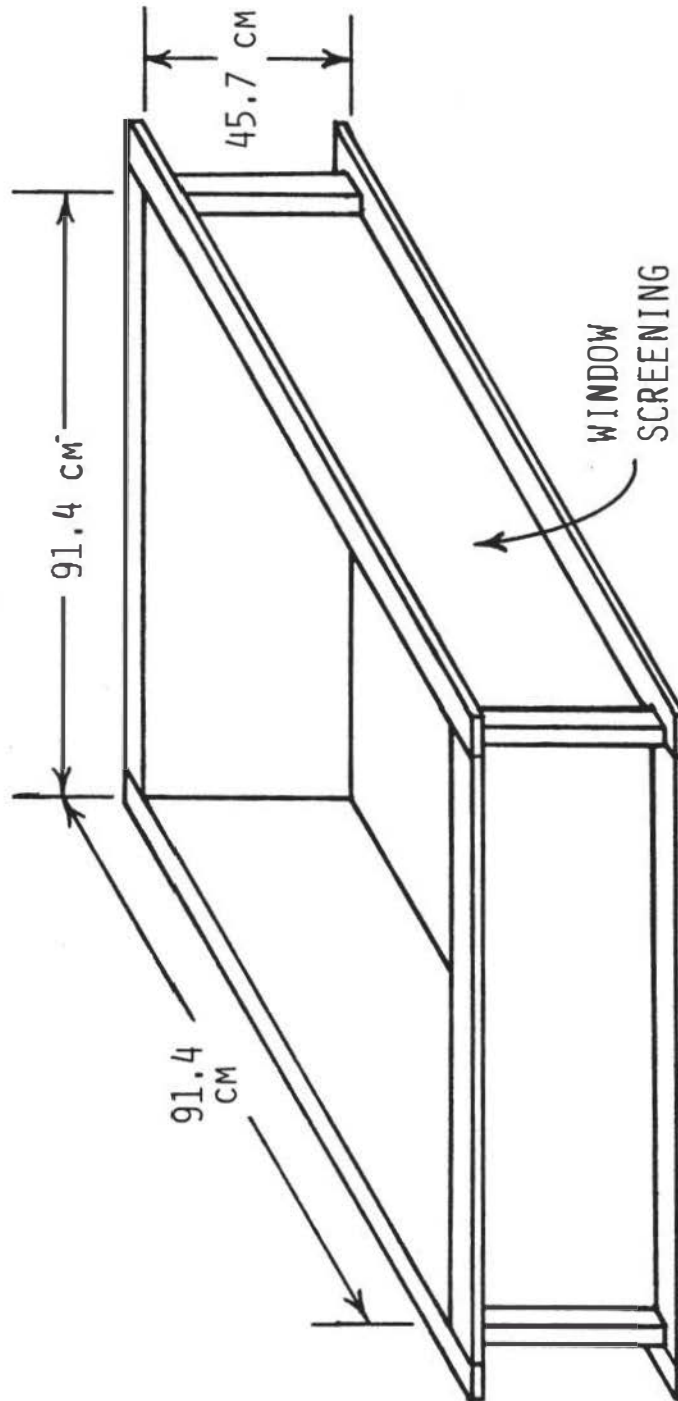
Appendix 1. A listing of all experiments included in this study, showing the apparatus used, acclimation times, run duration, and the number of runs performed. The number of runs in which structure was present is in parentheses.

Experiment	Apparatus	Acclim. time	Run time	# Runs
1. DEPTH PREFERENCE				
<u>Bufo</u> alone	depth tank	30 min	1 hr	9(2)
<u>Hyla</u> alone	depth tank	30 min	1 hr	4(2)
<u>Bufo</u> + <u>Dytiscus</u>	depth tank	30 min	1 hr	7(1)
<u>Hyla</u> + <u>Dytiscus</u>	depth tank	30 min	1 hr	4(2)
<u>Dytiscus</u> alone	depth tank	30 min	1 hr	6(1)
2. TADPOLE VULNERABILITY WITH DEPTH				
<u>Bufo</u>	depth tank	30 min	2 hr	4(2)
<u>Hyla</u>	depth tank	30 min	2 hr	4(2)
<u>Bufo</u> + <u>Hyla</u>	depth tank	30 min	2 hr	(2)
3. SUBSTRATE COLOR PREFERENCE				
<u>Bufo</u>	wading pool	15 min	30 min	6
<u>Hyla</u>	wading pool	15 min	30 min	6
<u>Dytiscus</u>	wading pool	15 min	30 min	8
4. TADPOLE VULNERABILITY WITH SUBSTRATE COLOR				
<u>Bufo</u>	two-color substrate tank	15 min	1 hr	3
<u>Hyla</u>	two-color substrate tank	15 min	1 hr	6
5. STRUCTURE PREFERENCE				
<u>Dytiscus</u>	wading pool	20 min	1 hr	3

Experiment	Apparatus	Acclim. time	Run time	# Runs
6. RELATIVE MOVEMENT				
Bufo alone	movement tank	15 min	15 min	15
Hyla alone	movement tank	15 min	15 min	10
Bufo + _Dytiscus_	movement tank	15 min	15 min	10
Hyla + _Dytiscus_	movement tank	15 min	15 min	10
Dytiscus alone	movement tank	10 min	15 min	5
Dytiscus + _Bufo_	movement tank	15 min	15 min	5
Dytiscus + _Hyla_	movement tank	15 min	15 min	5
7. TADPOLE VULNERABILITY IN THE FIELD				
Bufo alone	field enclosure	----	24 hr	3
Hyla alone	field enclosure	----	24 hr	3
Mixed	field enclosure	----	24 hr	6

Appendix 2. Gosner stages of tadpoles in all experiments.

Cat. #	Vol, $\bar{x}$ ml/tad.	Stages										Median Stage	Range
Bufo depth preference without structure													
B1	.11	35	36	38	38	38	38	38	38	38	38	38	35-38
B2	.11	35	37	38	38	38	38	38	39	39	40	38	35-40
B3	.12	35	35	37	37	37	37	38	38	38	39	37	35-39
B4	.11	32	34	36	38	38	38	39	39	39	40	38	32-40
B5	.08	31	32	34	35	35	36	36	36	36	38	35.5	31-38
B6	.11	35	36	36	36	37	37	38	38	38	39	37	35-39
B7	.13	31	33	34	35	35	36	36	37	37	37	35.5	31-37
Total	.11 (s.d.=.015)											37	31-40
Bufo depth preference with structure													
BS1	.13	33	36	36	36	36	37	38	38	38	39	36.5	33-39
BS2	.16	35	36	37	37	38	39	39	40	41	41	38.5	35-41
Total	.14 (s.d.=.018)											37.5	33-41
Bufo depth preference with a beetle present (see also BS2)													
BD1	.13	33	34	34	34	35	35	35	35	36	36	35	33-36
BD2	.11	32	33	33	34	34	34	34	35	35	37	34	32-37
BD3	.14	34	34	34	35	35	35	35	35	35	35	35	34-35
BD4	.06	28	28	29	29	29	30	31	31	32	33	29.5	28-33
BD5	.08	29	31	31	31	31	31	31	31	32	33	31	29-33
BD6	.13	33	33	34	34	35	35	35	35	36	36	35	33-36
Total	.11 (s.d.=.034)											34.5	28-37

Cat. #	Vol, $\bar{x}$ ml/tad.	Stages	Median Stage	Range
		Hyla depth preference without structure and		
		Hyla + beetle depth preference		
H3	.18	34 35 35 35 35 37 37 38 39 40	36	34-40
H4	.25	34 36 36 36 36 37 37 37 38 40	36.5	34-40
Total	.22 (s.d.=.049)		36.5	34-40
		Hyla depth preference with structure and		
		Hyla + beetle depth preference with structure		
H1	.16	31 31 32 33 36 36 36 36 36 36	36	31-36
H2	.18	34 35 35 35 35 35 36 36 40 40	35	34-40
Total	.17 (s.d.=.014)		36	31-40
		Vulnerability with depth experiment		
		Bufo without structure		
VD11	.10	33 33 33 34 35	33	33-35
VD12	.09	33 33 34 34 36	34	33-36
VD13	.10	31 33 34 35 35	34	31-35
VD21	.12	34 35 35 35 36	35	34-36
VD22	.12	33 35 35 35 35	35	33-35
VD23	.12	33 33 34 35 35	34	33-35

Cat. #	Vol, $\bar{x}$ ml/tad.	Stages	Median Stage	Range
Bufo with structure				
VD31	.12	34 35 35 35 36	35	34-36
VD32	.12	34 35 36 36 36	36	34-36
VD33	.14	33 34 36 36 36	36	33-36
VD41	.11	32 34 34 35 36	34	32-36
VD42	.12	31 35 35 36 36	35	31-36
VD43	.11	33 34 35 36 37	35	33-37
Hyla without structure				
VD51	.10	30 31 31 31 33	31	30-33
VD52	.10	28 29 30 30 33	30	28-33
VD53	.12	31 31 31 32 34	31	31-34
VD61	.13	29 29 33 34 34	33	29-34
VD62	.12	28 29 31 31 32	31	28-32
VD63	.12	29 29 31 31 33	31	29-33
Hyla with structure				
VD71	.12	28 29 31 32 32	31	28-32
VD72	.14	29 29 32 34 34	32	29-34
VD73	.12	29 29 31 31 36	31	29-36
VD81	.16	33 37 38 38 38	38	33-38
VD82	.14	29 34 36 37 37	36	29-37
VD83	.14	31 31 34 36 38	34	31-38

Cat. #	Vol, $\bar{x}$ ml/tad.	Stages										Median Stage	Range

Mixed runs with structure

VD91   B: .13   43 41 42   H: .16   37 37 37

VD92   B: .13   42 41 41   H: .18   36 37 36

VD93   B: .13   39 43 42   H: .16   40 39 37

VD101   B: .13   37 38 38   H: .20   39 37 37

VD102   B: .17   36 36 38   H: .23   37 37 36

VD103   B: .17   38 38 38   H: .26   36 39 37

Bufo grand total .12 (s.d.=.021)   35   31-43

Hyla grand total .15 (s.d.=.044)   31   28-40

Bufo substrate color preference

CB1 .09   33 33 33 33 34 35 36 36 36 38   34.5   33-38

CB2 .09   32 32 33 33 33 33 34 35 35 38   33   32-38

CB3 .10   32 32 32 33 34 35 36 37 38 38   34.5   32-38

CB4 .11   32 34 35 35 35 37 38 38 39 39   36   32-39

CB5 .11   33 33 33 33 33 34 34 36 38 38   33.5   33-38

CB6 .11   34 34 35 35 35 36 36 36 38 38   35.5   34-38

Total .10 (s.d.=.009)   34.5   32-39

Hyla substrate color preference

CH1 .17   33 34 35 36 36 36 37 37 37 37   36   33-37

CH2 .20   34 36 36 37 37 37 37 37 37 38   37   34-38

CH3 .14   29 30 30 31 34 35 35 35 35 37   34.5   29-37

CH4 .16   29 31 33 33 35 35 35 35 37 37   35   29-37

CH5 .15   29 31 35 35 36 36 37 37 37 37   36   29-37

Cat. #	Vol, $\bar{x}$ ml/tad.	Stages	Median Stage	Range
CH6	.16	29 30 31 31 32 34 37 37 37 37	33	29-37
Total	.16 (s.d.=.020)		35.5	29-38

Hyla vulnerability with substrate color

Cat. #	Vol, $\bar{x}$ ml/tad.	Stages	Median Stage	Range
VC1	.22	36 36 36 36 37 37 37 37 37 38	37	36-38
VC2	.14	29 30 31 31 31 31 33 33 35 35	31	29-35
VC3	.12	27 28 29 31 31 32 32 33 35 36	31.5	27-36
VC4	.10	28 28 28 28 28 28 30 31 31 36	28	28-36
VC5	.18	33 34 35 36 36 36 36 37 38 38	36	33-38
VC6	.15	31 31 31 31 32 33 35 35 36 37	32.5	31-37
Total	.15 (s.d.=.044)		32	27-38

Bufo vulnerability with substrate color

Cat. #	Vol, $\bar{x}$ ml/tad.	Stages	Median Stage	Range
VC7	.13	36 38 38 38 39 39 40 40 40 41	39	36-41
VC8	.11	36 36 37 38 40 41 42 42 42 42	40.5	36-42
VC9	.14	36 38 39 39 39 39 39 40 40 40	39	36-40
Total	.13 (s.d.=.015)		39	36-42

Bufo movement

Cat. #	Vol, $\bar{x}$ ml/tad.	Stages	Median Stage	Range
TM1	.07	31 31 33 33 33 33 33 33 34 35	33	31-35
TM4	.17	36 38 38 38 38 38 38 39 39 39	38	36-39
TM5	.10	41 41 42 42 42 42 43 43 43 44	42	41-44

Hyla movement

Cat. #	Vol, $\bar{x}$ ml/tad.	Stages	Median Stage	Range
TM2	.26	34 35 35 35 36 36 36 37 37 38	36	34-38
TM3	.25	33 35 35 35 35 35 35 36 37 38	35	33-38

Cat. #	Vol, $\bar{x}$ ml/tad.	Stages	Median Stage	Range

Bufo movement with beetle present

| TB1 | .13 | 34 38 39 39 40 41 41 41 42 43 | 40.5 | 34-43 |
| TB3 | .12 | 36 39 40 41 42 42 42 43 43 44 | 42 | 36-44 |

Hyla movement with beetle present

| TB2 | .13 | 32 32 33 33 34 36 36 36 37 37 | 35 | 32-37 |
| TB4 | .16 | 30 31 33 33 34 36 36 37 37 37 | 35 | 30-37 |

Beetle movement with Hyla present

| BM1 | .16 | 31 32 33 35 35 35 36 36 37 38 | 35 | 31-38 |

Beetle movement with Bufo present (see also TB3 and TB5)

| BM2 | .10 | 34 35 36 38 40 41 41 41 42 43 | 40.5 | 34-43 |
| TB5 | .13 | 36 38 38 38 39 39 40 40 40 41 | 39 | 36-41 |

Field experiment *

Single species density = 50

FV11	.13	Bufo: 33 remaining	41	37-44
FV22	.13	Bufo: 40 remaining	42	38-45
FV12	.18	Hyla: 39 remaining	38	33-41
FV23	.17	Hyla: 40 remaining	38	34-44

Single species density = 20

| FV33 | .16 | Bufo: 18 remaining | 41 | 39-44 |
| FV31 | .20 | Hyla: 17 remaining | 39 | 28-43 |

Cat. #	Vol, $\bar{x}$ ml/tad.	Stages	Median Stage	Range
Mixed Species Density = 50 (25 Bufo, 25 Hyla)				
FV21	B =.14	Bufo: 19 remaining	43	41-45
	H =.16	Hyla: 19 remaining	41	34-44
FV13	B =.14	Bufo: 13 remaining	41	37-43
	H =.18	Hyla: 18 remaining	39	32-43
Mixed Species Density = 20 (10 Bufo, 10 Hyla)				
FV32	B =.15	Bufo: 9 remaining	40	38-44
	H =.19	Hyla: 7 remaining	38	36-40
FV41	B =.16	Bufo: 10 remaining	42	38-44
	H =.21	Hyla: 7 remaining	36	34-41
FV42	B =.15	Bufo: 8 remaining	40.5	38-43
	H =.20	Hyla: 10 remaining	37.5	33-40
FV43	B =.13	Bufo: 8 remaining	41	38-43
	H =.21	Hyla: 10 remaining	39	32-41
Total Bufo	.14	(s.d.= 0.01)	41	40-43
Total Hyla	.19	(s.d.= 0.02)	38	36-41

* individual stages are not shown; all the tadpoles

remaining were staged