1999

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1999. *Transactions of the Nebraska Academy of Sciences*, 25: 73–76

MICROHABITAT PREFERENCES OF BULLFROG TADPOLES (*RANA CATESBEIANA*) OF DIFFERENT AGES

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ABSTRACT

I experimentally investigated the habitat use preferences of bullfrog (*Rana catesbeiana*) tadpoles of different ages (early, first-year vs. late, second-year, premetamorphic) in the laboratory. Early tadpoles showed a preference for non-vegetated areas, whereas late tadpoles showed no preference. Early tadpoles were seen more often over small, gravel substrate as opposed to large rocks, whereas late tadpoles showed no preference. Early tadpoles preferred medium depths, whereas later tadpoles preferred deeper water. Thus, it appears there may be habitat preferences in bullfrog tadpoles, and that these preferences may change over time.

† † †

Habitat selection by tadpoles appears to depend on many factors. Some studies suggest that habitat choice of tadpoles is influenced, at least to some extent, by previous experience with particular habitat characteristics (Wiens 1970, 1972), but this finding is not universal (Dunlap and Satterfield 1985). Other studies suggest that factors such as oxygen concentration, population density, water temperature and depth, vegetation density, and substrate type or pattern, and phototactic preference all play a role in at least some anuran larval habitat and microhabitat selection (e.g., Dunlap and Satterfield 1985; Jaeger and Hailman 1976; Johnson 1991; Noland and Ultsch 1981; Peterson et al. 1992; Waringer-Löschenkohl 1988; Wollmuth et al. 1987). In some cases there appear to be ontogenetic or size-related changes in the habitat preference and selection of tadpoles (see Alford 1986; Jaeger and Hailman 1976; Werner 1992).

Observations made while testing various means of trapping amphibian larvae (Smith and Rettig 1996), suggested that bullfrog (*Rana catesbeiana*) tadpoles showed a shift from living near a pond's edge to living in its center as they grew (see also Werner 1992). I conducted laboratory experiments on microhabitat selection in bullfrog (*Rana catesbeiana*) tadpoles at different ontogenetic stages to see if there were differences in habitat or microhabitat preferences in the laboratory. Based on the observations associated with the trapping study (Smith and Rettig 1996), I predicted that there would be (1) a preference for vegetated areas relative to non-vegetated areas early in ontogeny, (2) a preference for finer substrate (e.g., gravel) compared to coarser substrate (e.g., larger rocks) early in ontogeny, and (3) a preference for shallower waters over deeper waters early in ontogeny. In each case I predicted that larger, older tadpoles would prefer the opposite of the smaller, younger tadpoles.

MATERIALS AND METHODS

Tadpoles for these experiments were obtained from two sources. Early tadpoles were raised from field-collected egg masses laid in mid-June 1996 from southeastern Michigan (hatched ≈ 15–16 June 1996). Tadpoles were allowed to hatch and then were fed algal flakes *ad libitum* and kept in large plastic containers until used in the experiment. Second-year tadpoles were field-collected in a pond at the Kellogg Biological Station's experimental pond complex in southwestern Michigan using a bag seine on 7 July 1996. Early tadpoles were tested at ≈ 3 mm snout-vent length (SVL, measured using dial calipers) (tested 23 June 1996) and ≈ 7 mm SVL (tested 8–11 July 1996). Second-year tadpoles were ≈ 30–35 mm SVL, and two stages were tested: those without prominent hindlimbs, and those with prominent hindlimbs (stage 35–38; Gosner 1960) (tested 9–11 July 1996). Tadpoles were released at the conclusion of the experiment.

Three sets of experiments were conducted to assess tadpole preferences for three habitat variables. Experiment 1 considered habitat selection for the presence or absence of vegetation with half of the aquarium filled with plastic plants and half left as open water. Experiment 2 compared habitat preference for two substrate types, gravel and rock, in which half of the bottom of the aquarium was covered with small gravel (≈ 3–5 mm diameter) and the other half was covered with larger rocks (≈ 25–35 mm in diameter). Experiment 3 examined tadpole preferences for different water depths by elevating one end of the aquarium using a brick to give a water depth gradient from 40 mm to 130 mm. In this experiment I divided the aquarium into thirds (shallow, medium, deep) to quantify tadpole behavior. I used chi-square analysis to compare tadpole class responses in each experiment.

All experiments were conducted in 10-gallon (≈ 37 L; 30 cm high × 26 cm wide × 50 cm long) aquaria with 100 mm deep unfiltered pond water (three aquaria were used simultaneously) and followed the same general procedure. These experiments were performed at the Kellogg Biological Station's Experimental Pond Facility. A single tadpole was placed in the middle of the aquarium (except for Experiment 3, in which the tadpole was placed either ⅓ of the way from the shallow end, or ⅓ of the way from the deep end). The tadpole's location was then checked 15 min later (preliminary observations suggested this was long enough for the tadpoles to fully explore the aquarium). Lighting and temperature of the aquaria were ambient, and the orientation of the treatments was varied between aquaria so as to eliminate any potential biases. For the 3 mm, 7 mm, and second-year tadpoles without hindlimbs, 24 individual tadpoles were used per experiment per size class, and 18 tadpoles were used for the second-year tadpoles with hindlimbs. Early tadpoles (3 mm and 7 mm) and second-year tadpoles without hindlimbs were used once in only one set of experiments, whereas the second-year tadpoles with hindlimbs were used once in each set of experiments (due to the small numbers collected).

RESULTS

Experiment 1 (see Fig 1A): For the small tadpoles, there appeared to be a preference for the non-vegetated side of the aquarium (3 mm: df = 1, $\chi^2 = 6.0$, $P < 0.025$; 7 mm: df = 1, $\chi^2 = 8.5$, $P < 0.005$), whereas for the large second-year tadpoles, there did not appear to be a preference (without hindlimbs: df = 1, $\chi^2 = 2.7$, $P > 0.1$; with hindlimbs: df = 1, $\chi^2 = 0.9$, $P > 0.1$).

Experiment 2 (see Fig. 1B): Smaller individuals tended to occur on the gravel side more often than on the rock side (3 mm: df = 1, $\chi^2 = 6.0$, $P < 0.025$), and were often seen in the interstices between the pieces of gravel. None of the other stages showed a preference ($P > 0.1$ in all cases).

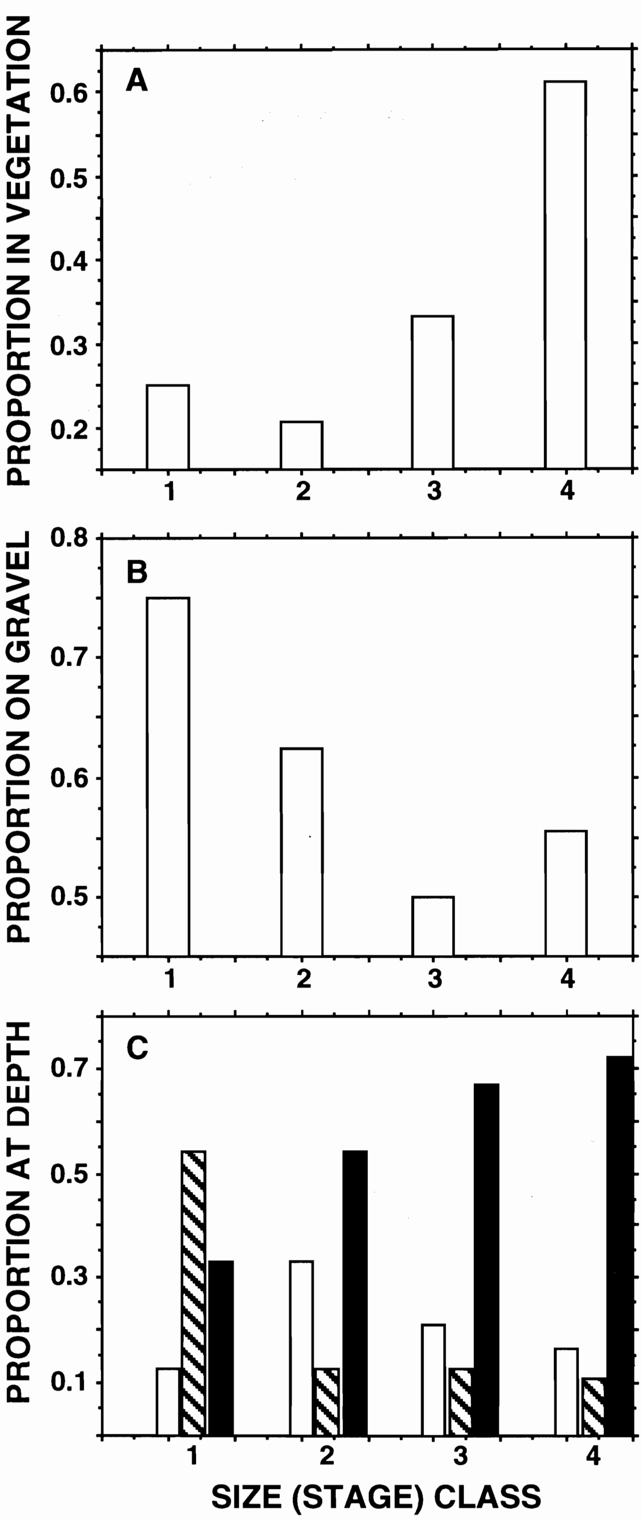

Figure 1. The proportion of various size classes of bullfrog (*Rana catesbeiana*) tadpoles using (A) the vegetated portion of an aquarium, (B) gravel substrates, and (C) the shallow (open bars), medium (striped bars), and deep (closed bars) portions of the aquarium. Size (Stage) Class 1 ≈ 3 mm SVL, Size (Stage) Class 2 ≈ 7 mm SVL, Size (Stage) Class 3 = second-yr tadpoles without prominent hind limbs, and Size (Stage) Class 4 = second-yr tadpoles with prominent hind limbs.

Experiment 3 (see Fig. 1C): Smaller individuals tended to be at medium depths (3 mm: df = 2, $\chi^2 = 6.25$, $P < 0.05$; 7 mm: df = 2, $\chi^2 = 6.25$, $P < 0.05$). Older, larger individuals tended to be seen in deeper water (without hindlimbs: df = 2, $\chi^2 = 12.25$, $P < 0.005$; with hindlimbs: df = 3, $\chi^2 = 12.34$, $P < 0.005$).

DISCUSSION

Tadpoles often change their behavior during the course of their development. For example, the temperature selected by *Rana cascadae* decreased with increasing developmental stage (Wollmuth et al. 1987). In *R. utricularia*, Alford (1986) found that the distribution of tadpoles among substrate type and vegetation density varied with size. In this study, bullfrog tadpoles of different ages and developmental stages appeared to show differences in all three habitat traits examined (vegetative cover, substrate size, and depth). Some of these differences are similar to patterns seen in field settings. In my experiment, as hypothesized, larger tadpoles tended to use deeper water, which mirrors the shift of larger, older bullfrog tadpoles to deeper habitats in natural ponds (Werner 1992).

Why did tadpoles of different age differ in habitat use? Size may be an important factor. For many amphibian larvae, increasing size decreases susceptibility to predation by both vertebrate and invertebrate predators (either through a size refugium or through increased unpalatability) (e.g., Travis et al. 1985). Thus, as tadpoles get bigger, they may be able to shift safely into the deeper water column where predation risk may be higher (see Lawler 1989; Werner and McPeek 1994). There may also be shifts in microhabitat use associated with changes in physiological preferences. Bullfrog-tadpole thermal preferences change with ontogeny (Hutchison and Hill 1978), and thus the observed changes in microhabitat use may reflect these changes in thermal preferences (see Noland and Ultsch 1981; Wollmuth et al. 1987).

The results for vegetation cover appear to be counter-intuitive, and contradict my original hypothesis. In this experiment, small tadpoles, presumably more susceptible to predation (e.g., Travis et al. 1985), appeared to prefer non-vegetated areas of water, whereas larger tadpoles showed no preference. If driven by predation risk, smaller tadpoles might be expected to use the vegetated areas more than the non-vegetated areas because they may provide a refuge from predators. I suggest three alternative, but not mutually exclusive, explanations. First, the presence of some tadpole predators may be higher in structurally complex habitats like aquatic vegetation (for aquatic invertebrates see Thorp and Covich 1991) such that smaller tadpoles avoid these habitats. Second, vegetated habitats in nature (or in this experiment) may not have the appropriate physical characteristics for small tadpoles (e.g., temperature, oxygen content). Third, my use of plastic aquarium vegetation may not be a true test of tadpole preference, but instead may have induced an aversion to a novel environment.

The addition of predators to any of the experiments could have resulted in different microhabitat preferences than those observed in this study. Predators are known to influence tadpole behavior and microhabitat selection. For example, *Hyla andersonii* tadpoles used benthic habitats more often in the presence of predators than in their absence (Lawler 1989). *Hyla versicolor* and *Rana sylvatica* responded to predators by not having a preference for a specific microhabitat in their presence, whereas in the absence of predators they both preferred the most structurally complex microhabitat which was also the predators' preferred microhabitat (Formanowicz and Bobka 1989). However, some of the preferences seen in my experiment may already reflect predator pressures, and may reflect evolved behavioral traits to avoid predators. For example, small tadpoles used the gravel in such a way as to be virtually invisible (e.g., motionless and down in the interstices of the gravel).

My experimental design does not allow me to analyze for ontogenetic shifts in habitat use because the early tadpoles and later tadpoles had different past experiences. The early tadpoles were raised in plastic containers whereas the later tadpoles were raised under natural conditions. Thus the differences observed in this study may be the result of differences in experience. However, my results do suggest that additional investigations into the effects of age and experience would help us understand habitat use and selection of anuran larvae.

In conclusion, bullfrog tadpoles appear to express preferences for specific microhabitat characteristics (substrate type, vegetation cover, and depth). These preferences were seen in naive tadpoles (reared in plastic containers), suggesting they were not learned (at least in the two small size classes used here). Preferences also changed with tadpole size, possibly suggesting potential changes in microhabitat use within the aquatic stage.

ACKNOWLEDGMENTS

I thank J. Chase and M. Leibold for providing the early tadpoles, and J. Rettig for her assistance and support. J. Rettig and anonymous reviewers greatly improved the manuscript with comments on an early version of this manuscript, and A. Frahm and M. Cadd helped with an earlier draft. The Kellogg Biological Station of Michigan State University and G. Mittelbach generously provided me with facilities and equipment.

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