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Habitat of Origin and Changes in Water Chemistry Influence Development of Western Chorus Frogs

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ABSTRACT.—**A variety of biotic and abiotic variables have been shown to affect length of larval period and size of juveniles at metamorphosis in amphibians. However, influence of water quality on phenotypic plasticity of growth and development of tadpoles generally has received less attention. We examined how abiotic factors in the larval environment change over time and how these changes affect the growth and development of larval amphibians. Western Chorus Frogs, *Pseudacris triseriata*, in tallgrass prairie breed in ephemeral aquatic habitats including intermittent streams and bison wallows. Our objectives were to determine whether abiotic factors in the larval environment of *P. triseriata* changed predictably as pools dried and to determine whether these changes affected growth and development of tadpoles when the environment was simulated in the laboratory. In our field studies, pH increased gradually in wallows, whereas ammonium increased in streams, as each habitat dried. In the laboratory, we examined the effects of increased levels of pH and ammonium on growth and development of tadpoles collected from both wallows and streams. Tadpoles collected from streams metamorphosed significantly faster in the high ammonium treatment than tadpoles from wallows. In contrast, tadpoles from wallows metamorphosed faster in the high pH treatment than tadpoles collected from streams. Growth rates of tadpoles from streams were not significantly affected by high pH, whereas those from wallows were not significantly affected by high ammonium treatments. We suggest that changes in abiotic factors over the course of the larval period may influence developmental rate and that natal habitat may determine how tadpoles respond to changes in abiotic factors.**

Larvae of amphibians that breed in ephemeral aquatic habitats may experience a wide range of environmental variation that includes daily fluctuations in physiochemical properties and sudden decreases in water volume (Schmuck et al., 1994; Scholnick, 1994). Organisms that exploit ephemeral aquatic habitats must have adaptations to cope with such variation. One possible evolutionary response to environmental variability is for a species to be phenotypically plastic (Van Buskirk et al., 1997). Plasticity in length of larval period, size of juveniles at metamorphosis, and other morphological variation caused by both abiotic and biotic factors present in the developmental environment have been well documented for anurans. For example, growth and developmental rates of tadpoles are affected by biotic factors such as presence of predators (*Bufo americanus*: Skelly and Werner, 1990; *Pseudacris triseriata*: Sredl and Collins, 1991; *Rana sylvatica*: Van Buskirk and Yurewicz, 1998) and low availability or quality of food (*Hyla regilla, Rana boglii, Rana catesbeiana*: Kupferberg, 1997; *R. catesbeiana, Xenopus* spp.: Wassersug, 1997; *Rana pipiens*: Glennemeier and Denver, 2002). Growth and developmental rates also are affected by abiotic factors such as increased temperature (*Rana clamitans, R. pipiens, R. sylvatica*: Smith-Gill and Berven, 1979; *Bufo boreas*: Hayes et al., 1993; *Scaphiopus couchii*: Newman and Dunham, 1994; *Rana temporia*: Olsson and Uller, 2002) and rate of desiccation of habitat (*Hyla pseudopuma*: Crump, 1989; *Scaphiopus hammondii*: Denver et al., 1998; *Hyla cinerea, Hyla gratiosa*: Leips et al., 2000; *Rana* spp.: Parris, 2000). However, the ability to respond to some abiotic and biotic factors can vary depending upon the size or stage of tadpoles at the time of exposure (for a review, see Denver, 1997).

Abiotic factors generally considered to assess water quality (e.g., pH and concentrations of dissolved oxygen, soluble reactive phosphorus, nitrate, nitrite, and ammonium) can change dramatically over the course of the larval period (Cole, 1994; Schmuck et al., 1994; Scholnick, 1994). Dissolved oxygen can cycle diurnally with photosynthesis and respiration; however, dissolved oxygen also can decrease as habitats dry or over the growing season because of a decrease in the abundance of algae or decreased mixing in flowing systems (Bronmark et al., 1991; Holomuzki, 1998). Diurnal cycling also may occur in pH in response to the relative levels of dissolved oxygen and carbon dioxide, but pH also may increase over time in response to the concentration of calcium carbonate as water evaporates. Increases in ammonium also have

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been associated with drying habitats as nitrogenous animal wastes are concentrated by decreased volume (Wright and Wright, 1996). Decreased levels of dissolved oxygen can also increase levels of ammonium, as ammonium is the dominant form of nitrogen under anoxic conditions (Dodds, 2002).

Changes in water quality generally have received less attention regarding their effects on tadpole growth and development than biotic factors. Exceptions include studies on effects of concentrations of various forms of nitrogen generally because of interest in the effects of fertilizers (Allran and Karasov, 2000; Nebeker and Schuytema, 2000; Hatch and Blaustein, 2003) and pH levels because of interest in the effects of acid rain (Cummins, 1989; Watkins-Colwell and Watkins-Colwell, 1998). Abiotic factors that are correlated with the predictability of the environment are indicators of habitat condition and, therefore, may act as cues for the onset of metamorphosis in the larvae of aquatic organisms. Changes in abiotic factors also may have direct effects on larval amphibian physiology (Wright and Wright, 1996; Ultsch et al., 1999).

We chose the Western Chorus Frog, *P. triseriata*, as a model to study the effects of natal habitat type and its associated abiotic environment on growth and development of tadpoles. Chorus frogs are small hylid frogs distributed throughout much of central and eastern North America (Conant and Collins, 1998). *Pseudacris triseriata* in the Flint Hills region of Kansas breed in many ephemeral habitats including intermittent streams and bison wallows. Wallows are shallow concave depressions formed when bison (*Bos bison*) roll repeatedly in the same location. Hydroperiods in these two habitats range from days to weeks in bison wallows (Gerlanc and Kaufman, 2003) and 2–10 months in intermittent streams (Tate, 1990). Tadpoles of *P. triseriata* generally metamorphose within two months of egg deposition, but plasticity in developmental time and growth rates have not been examined previously in these habitats (Collins, 1993).

The objectives for the field portion of our study were to determine whether abiotic factors in the larval environment of *P. triseriata* changed predictably as wallows and streams dried and to determine how any abiotic changes affected tadpole growth and development in these environments. We hypothesized that at least a subset of abiotic factors would change predictably with habitat desiccation in each environment (Black, 1976; Wright, 1985; Williams, 1987). If abiotic factors changed predictably with habitat desiccation, we expected correlated responses in growth and development of the tadpoles either as an adaptive response to habitat degradation or as a result of nonadaptive physiological responses.

The objectives of the laboratory portion of our study were to examine the effects of a subset of abiotic factors found to change significantly throughout the hydroperiod during the field study. Because bison wallows and intermittent streams were very different in terms of hydrology and water chemistry, we also examined whether habitat of origin affected the response of tadpoles to abiotic factors in a controlled environment. Specifically, we expected tadpoles from both wallows and streams to react adaptively to the factors that changed predictably in their natal habitat by increasing their developmental rates.

Materials and Methods

Study Site

Konza Prairie Biological Station is a 3487 ha native tallgrass prairie located in the Flint Hills of eastern Kansas (39°05'N, 96°35'W). The topography of Konza Prairie is characterized by flat hilltops that grade into steep slopes with limestone outcrops and valley lowlands (Oviatt, 1998). Vegetation is dominated by a few C_4-grass species that include big bluestem (*Andropogon gerardii*), little bluestem (*Andropogon scoparius*), Indian grass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*; Freeman, 1998). Aquatic habitats on Konza Prairie include streams that occur in one of five drainage basins and 12 permanent ponds (Oviatt, 1998). The upper reaches of all streams in these basins are intermittent. Bison wallows and other pools that form in various depressions during spring rains represent ephemeral aquatic habitats. For a more detailed description of Konza Prairie including sample site descriptions, see Gerlanc (1999).

Each study site was used as a breeding site by *P. triseriata*, and each site dried completely at some time during the growing season. We sampled 18–25 bison wallows across 12 experimental areas each year. Nine of these experimental areas were within the 949-ha bison enclosure. The remaining three experimental areas were outside of the fenced bison area and were relic bison wallows. Although bison have not used these relic wallows during the last 125 yr (Knapp et al., 1999), hydroperiod and water chemistry in relic wallows were similar to that found in active wallows (Gerlanc and Kaufman, 2003). The range of volume of water in wallows, as calculated from maximum length, width, and depth measurements, was 0.03–31.13 m^3, mean = 3.95 m^3 during the study. We added five intermittent stream sites to the study in 1997 and five more in 1998 for a total of 10 stream sites. All 10 intermittent streams typically flowed 2–10 months per year (Tate, 1990).

Field Study

Water Sampling.—We collected water samples weekly after we found the first egg masses and

increased sampling up to several times per week once sample sites began to dry. We defined the hydroperiod for each sampling site as the number of days from when the first egg masses were found until the pool dried. Sampling of sites began before dawn to try to minimize the effect of photosynthesis on the concentration of dissolved oxygen in the water. On each sampling day, we chose a starting site at random. From that site, a coin flip determined the direction in which the sampling would proceed from the original location. The remaining sites were sampled sequentially in that direction. We could not sample in a completely randomized order because of the time required to travel the distance from site to site.

At each site, we measured water temperature, ambient temperature, and dissolved oxygen (YSI model 51B oxygen meter; Yellow Springs Instrument Co., Inc). We collected water samples for chemical analyses in acid-washed bottles from the same place at each site on each sample day, and measured maximum length, maximum width, and maximum depth of each site. Water samples were kept in a cooler until they were brought back to the laboratory. In the laboratory, we measured pH by using a Markson model 93 digital pH/MV meter (Markson Science), filtered water samples (Whatman GF/C filters), and stored water samples at –20°C for further analyses. In 1997 and 1998, we added analyses of nitrate, ammonium, and soluble reactive phosphorus to get a more complete understanding of changes in water quality. We determined nitrate concentration by the cadmium reduction method, ammonium concentration by the indophenol method, and soluble reactive phosphorus concentration by the phosphoantimonyl-molybdenum complex method (Eaton et al., 1995).

Tadpole Sampling.—In each year of the study, sample sites were checked for chorus frog activity during the last two weeks of February or when weather became favorable for emergence, chorusing, or breeding (rain events or temperatures above 5°C; Collins, 1993). When chorus frogs started to call, we checked sample sites daily for the presence of egg masses. Once egg masses were found, we continued to monitor the development of the eggs until they hatched. We sampled tadpoles after hatching and then once per week at each sample site in each year of the study. Sampling was increased up to several times per week once sample sites began to dry.

We collected tadpoles from wallows and streams by sweeping a dip net through the water for 3 min. We kept 15–30 tadpoles from each sample to obtain data on snout–vent length (SVL), dry body mass, and developmental stage of the tadpoles. We euthanized all sampled tadpoles by immersion in a 50 mg/L solution of benzocaine followed by freezing (Schaeffer et al., 1991; Andrews et al., 1993). Tadpoles were stored at –20°C for up to six months until time was available to measure, weigh, and stage (Gosner, 1960) them.

Statistical Analyses.—We calculated growth and developmental rates of tadpoles for each sample site by subtracting the mean size or mean stage of tadpoles collected on a given sample date from the mean size or mean stage of tadpoles collected on the previous sample date. The difference was divided by the number of days between sample dates such that all rates were in gram/day or stages/day. Rates were calculated for each intermittent stream site and then averaged among sites for each pair of sample dates. Because dry body mass and SVL were tightly correlated ($r = 0.88$, df = 528, $P = 0.0001$), we chose to use change in dry body mass as the measure of growth for all analyses. Data for all measurements were not significantly different from a normal distribution (Shapiro-Wilk *W*-test). We were unable to calculate growth rate or developmental rate for tadpoles in wallows, because wallows dried between sample dates, which prohibited us from collecting successive samples. Thus, we could not make direct comparisons between wallow and stream tadpoles.

Data collected in the field were repeated measures across time. Consequently, we analyzed the data by using a mixed repeated-measures ANOVA. Days since first hatching were treated as fixed effects and sites were treated as random effects. We analyzed the effects of time in days since first hatching on the growth and development of the tadpoles. Similar analyses were done on water chemistry data to assess changes that occurred in abiotic factors during the larval period. Data were pooled across sites within each habitat type within each year of collection unless otherwise specified. If mixed model analyses indicated significant overall differences, preplanned pairwise comparisons were made. Days compared for wallows included the beginning and end of the larval periods in 1996 and 1998.

We used Pearson correlation coefficients to analyze relationships among water depth, dissolved oxygen, ammonium, pH, time of day samples were collected, water volume, water temperature, developmental stage, dry body mass, and time in days since eggs hatched. We transformed data that were curvilinear to natural logs before conducting correlation analyses. We used the stepwise regression procedure to find the best regression models for predicting changes in abiotic factors. Variables with *P*-values > 0.15 were excluded from the models (SAS/STAT Users' Guide Institute, Inc., Cary, NC, 1990). We also used the stepwise regression procedure to model growth, as measured by dry body mass,

and developmental stage of the tadpoles of *P. triseriata* over time (dependent variables), by using measured abiotic factors averaged among stream sites within a sample day (independent variables). Although some of the abiotic variables measured were collinear, the correlations were not strong enough to require the use of other modeling techniques such as principal components analysis (Scheiner and Gurevitch, 1993).

Laboratory Study

Tadpole Sampling.—We collected tadpoles for the laboratory experiment within 24 h after hatching. Sixty tadpoles were pooled from three separate wallow sample sites selected because they each contained a single cohort of tadpoles of the same age. Similarly, 60 tadpoles were pooled from five separate stream sites. Individuals were collected from multiple field sites for each habitat type to minimize bias in results caused by sibship effects (Leips et al., 2000; Richardson, 2002).

Experimental Design and Maintenance.—On the day of collection, we staged the development of each tadpole according to Gosner (1960) with the aid of a dissecting microscope. We used vernier calipers to measure snout–vent length (SVL) to the nearest 0.05 mm. To minimize stress, tadpoles were submerged in water during staging and measurement. We weighed each tadpole to the nearest 0.1 mg to determine wet body mass. We maintained tadpoles at 14°C in water from their pool of origin until each individual was measured, staged, placed into its own cup, and allocated to one of three treatments. Only tadpoles at Stage 25 were used for the experiment.

Experiments were conducted in an environmental chamber at 20°C ± 0.5 and 15:9L:D photoperiod. These conditions were typical of those experienced by tadpoles in their natural habitat. Each tadpole was placed alone in a numbered plastic cup (11.5 cm diameter × 14.5 cm deep), which was filled with 450 mL of water collected from a permanent stream that had ammonium levels from 0 to 0.03 mg/L. We used 0.1 N hydrochloric acid to adjust the pH to 7.41 ± 0.04. We monitored pH and ammonium daily by using a pH meter and a Hach ammonia-nitrogen test kit (range 0–3.9 mg/L, as ammonium ion; model NI-8, Hach Co.). We changed water as needed to maintain specified levels of pH and ammonium. Each tadpole was given 0.0045 g of a 3:1 mix of ground rabbit chow and Tetra Min flakes every three days. The amount of food we used was based on mass specific rations used by Alford and Harris (1988) and Skelly and Werner (1990) for their high food level treatments (ration in grams = [3/20] × [wet body mass of tadpole] × [number of days until next feeding]).

When tadpoles reached Stage 28, 30 tadpoles, 15 from each habitat (wallow or stream), were each assigned randomly to one of two treatments or a control for a total of 45 tadpoles used from each habitat type. The two treatments were high pH and high ammonium. These two factors were selected for study because they did not cycle diurnally, changed consistently with changes in water volume, and appeared to influence growth and development of tadpoles in the natal habitats (see Results). Treatments of ammonium and pH were increased to levels similar to those that occur in streams and wallows, respectively, as these ephemeral pools dry. In the high pH treatment, pH was increased from 7.57 ± 0.20 to 8.15 ± 0.30 by a one-time addition of 0.1 N sodium hydroxide. We were unable to maintain ammonium at the level (0.03 mg/L) of the water collected from the permanent stream because of rapid changes in ammonium caused by the small volume of cups. Therefore, ammonium was maintained at 0.81 mg/L ± 0.34 in all treatments except the high ammonium. The control level of ammonium, although higher than that in fresh stream water, overlapped with the natural range of ammonium found in flowing streams (Gerlanc and Kaufman, 2003). The high ammonium treatment was increased to 1.85 mg/L ± 0.65 by a one-time addition of 0.1 N ammonium chloride and was based on the average peak levels of ammonium seen after flow stopped and stream sites began to dry.

We randomly assigned three cups, each with a single tadpole, for each treatment and the control, to one of five shelves in the environmental chamber (18 cups per shelf). We monitored water quality daily and changed water as necessary to maintain treatment and control conditions. We increased food rations as the wet body mass of the tadpoles increased. Once a week, we randomly selected five tadpoles from each treatment to be weighed, staged, and measured.

As each tadpole completed metamorphosis (forelimb emergence, Stage 42), it was euthanized and stored as described above for the field study until time was available to measure and weigh it. We dried tadpoles in a drying oven at 60°C until body mass remained constant (about 48 h) to determine dry body mass.

Statistical Analyses.—We were able to obtain accurate measurements of SVL for hatchlings of *P. triseriata* at the time of collection. Measurements of wet body mass in tadpoles < 13 days old were less accurate because of excess water that we were not able to blot from the tadpoles without causing injury. SVL was correlated strongly with wet body mass ($r = 0.96$, df = 293, $P = 0.0001$), and because habitat of origin did not differentially affect the relationship between SVL and wet body mass ($F_{162,318} = 2.57$, $P = 0.25$), we used SVL as our measure of body size in all statistical analyses. Data for all

measurements were not significantly different from a normal distribution (Shapiro-Wilk *W*-test).

We analyzed the experiment with a two-way analysis of variance with repeated measures. Data were tested for the effects of treatment, tadpole habitat, and time in days since hatching. Analyses were done for both growth (SVL) and development (stage) of the tadpoles. Mixed model analyses for developmental stage were performed only on days 13, 19, 27, and 33 because all tadpoles were at Stage 25 at the beginning of the experiment and at Stage 42, metamorphosis, at the end. We analyzed the effects of treatment and origin on larval period (measured as number of days from hatching to Stage 42) and SVL at metamorphosis using a two-way ANOVA with a completely randomized block design. In both analyses, data were pooled where nonsignificant differences occurred. If an ANOVA indicated significant overall differences, preplanned pairwise comparisons were made. All analyses were conducted with Statistica 6.0 (Statsoft) or SAS 8.0 (SAS Institute, Inc., Cary, NC, 1990).

Results

Field Study

Hydroperiod and Abiotic Factors.—Spring rains filled bison wallows twice in 1996, 10 May and 26 May, while *P. triseriata* were breeding. Eggs were found in wallows within 24 h of precipitation events. In 1997 and 1998, bison wallows filled several times and held water for short periods of time (range: 2–12 days) from February to June. *Pseudacris triseriata* only used the wallows in early April during 1997 and 1998. During the breeding period of *P. triseriata*, individual wallows did not hold water for the same period of time; no bison wallow held water longer than 26 days. Regardless of the hydroperiod of each individual wallow, pH of the water in wallows increased as the volume of water decreased ($r = -0.53$, df = 110, $P = 0.0001$; Fig. 1). Individual wallows showed the same pattern as they dried, although the correlation only approached significance (e.g., wallow 4: $r = -0.80$, df = 5, $P = 0.06$). Water temperature (range: 10.0–25.4°C, mean = 18.9) was the only other abiotic factor that changed relative to the volume of water in the wallows ($r = -0.26$, df = 109, $P = 0.01$).

Intermittent streams, filled from rainfall in the previous fall and winter, were available to *P. triseriata* for chorusing and breeding earlier than wallow sites in all years of the study. *Pseudacris triseriata* began to chorus around intermittent streams in March in both 1997 and 1998. The hydroperiod of intermittent stream sites used by *P. triseriata* ranged from 84–102 days in 1997 and from 57–67 days in 1998. In 1997, no abiotic factors that were measured changed

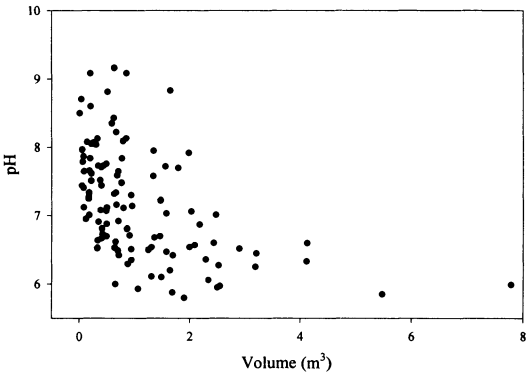

FIG. 1. The relationship between pH and volume of water in bison wallows on Konza Prairie Biological Station, Kansas. Data were pooled for 1996, 1997, and 1998.

relative to depth or volume of intermittent streams when stream sites were pooled (Fig. 2A–C). However, when individual stream sites were analyzed separately, levels of ammonium increased and levels of dissolved oxygen decreased just before each of the five intermittent streams sites dried (e.g., site G for ammonium: $r = -0.71$, df = 8, $P = 0.03$; dissolved oxygen: $r = 0.94$, df = 7, $P = 0.005$). Levels of ammonium in intermittent stream sites with flow were significantly lower than levels of ammonium where water flow had stopped in the intermittent sections ($t = -8.47$, df = 30, $P = 0.001$; Fig. 2A). Levels of dissolved oxygen decreased significantly before intermittent streams dried ($t = 4.49$, df = 20, $P = 0.0002$; Fig. 2A). Water temperature increased significantly from when eggs were laid (~10°C) until the streams dried (~20°C; $t = -5.62$, df = 26, $P = 0.0002$; Fig. 2B).

Ammonium levels were more variable in 1998 (Fig. 2D) than in 1997 (Fig. 2A). Greater fluctuations in ammonium may be caused by the dilution that resulted from input of water during several rain events in 1998, which occurred during the larval period (12, 15, and 19 May, total rainfall = 22.8 mm). Levels of ammonium in intermittent streams before rain events were significantly higher than in intermittent streams after rain events ($t = 2.14$, df = 98, $P = 0.03$), whereas stream depth was not altered significantly by the same precipitation events (Fig. 2E; $t = 1.35$, df = 73, $P = 0.18$). Levels of ammonium and water temperature increased significantly at the end of the hydroperiod relative to levels when eggs were laid (ammonium: $t = -2.12$, df = 105, $P = 0.04$; temperature: $t = -8.24$, df = 71, $P = 0.0001$). In contrast, dissolved oxygen was significantly lower as streams dried (Fig. 2D; $t = 7.93$, df = 71, $P = 0.0001$). No other abiotic factors (e.g., pH, nitrate, or soluble reactive phosphorus) were

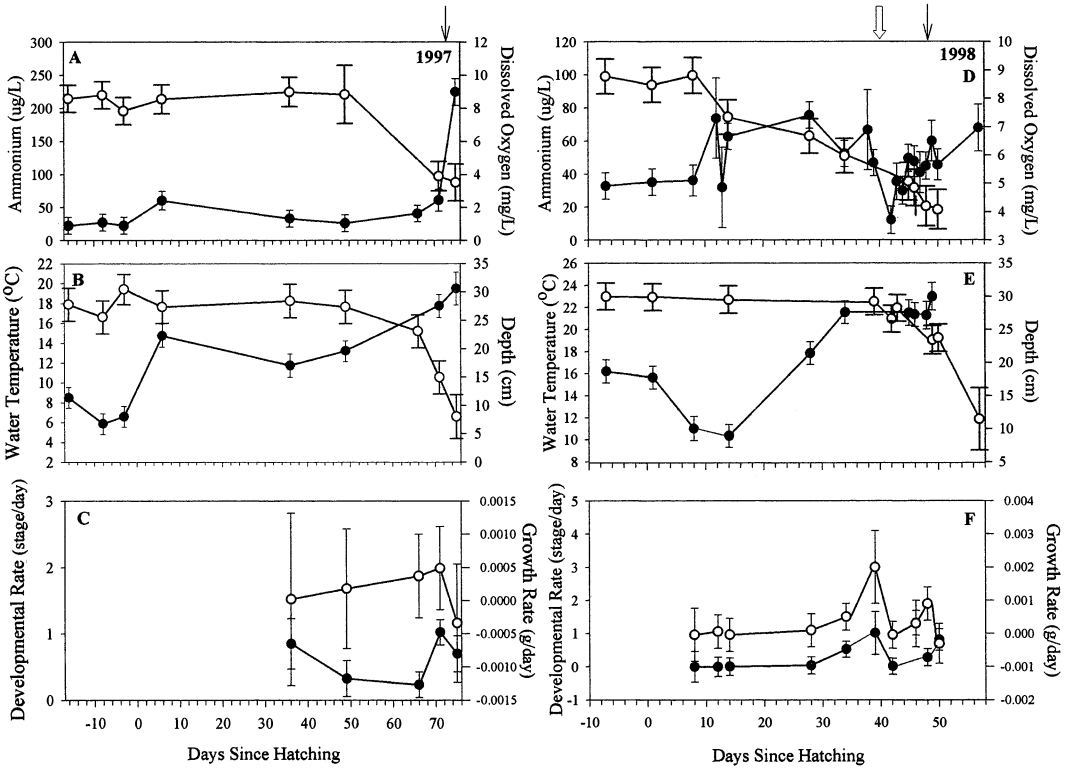

FIG. 2. Abiotic factors measured in 1997 (A–C) and 1998 (D–F) in intermittent streams during breeding season and larval period of the Western Chorus Frog (*Pseudacris triseriata*) on Konza Prairie Biological Station, Kansas. Data were averaged across five intermittent stream sites on each sample day in 1997 and 10 intermittent stream sites on each sample day in 1998. Bars represent ± 1 SE. In graphs A and D, closed circles represent ammonium and open circles represent dissolved oxygen. In graphs B and E, closed circles represent water temperature and open circles represent depth. In graphs C and F, closed circles represent tadpole developmental rate (Gosner stages), and open circles represent tadpole growth rate as measured by dry body mass. Line arrows indicate the point when water flow in intermittent stream sites stopped. The block arrow indicates the occurrence of rain during the larval period of *P. triseriata*. The last datapoint on each graph represents the last sample taken before intermittent stream sites dried completely.

correlated with depth in intermittent streams whether pooled among sites or analyzed within individual sites. In both years, pH was stable (mean = 7.48 ± 0.028) throughout the hydroperiod in all intermittent stream sites.

Growth and Development of Tadpoles.—Eggs laid in bison wallows on 11 May 1996 hatched within eight days. The hatching period was reduced to only four days for eggs laid when wallows filled the second time on 27 May 1996. Egg masses were first observed in bison wallows on 16 April in 1997 and on 13 April in 1998. Eggs in wallows hatched within five days of being laid in 1997 and within four days of being laid in 1998. Egg masses in intermittent streams were first observed on 9 March in 1997 and on 27 March in 1998. Eggs in streams hatched in 14–17 days in both years.

Growth rate of tadpoles in streams increased steadily throughout the larval period (growth rate ranged from 0.1–3 mg/day) in 1997, until the flow of water in intermittent streams stopped (Fig. 2C). Developmental rate fluctuated during the larval period, increasing just before and decreasing just after flow stopped in the intermittent streams (developmental rate ranged from 0 - 1.7 stages/day). Developmental changes approached statistical significance (Fig. 2C; $F_{4,8} = 3.51$, $P = 0.06$).

In 1998, both growth and developmental rates of tadpoles increased gradually (growth rate ranged from 0.1–0.4 mg/day and developmental rate ranged from 0–2.6 stages/day) during the larval period. Rain events did not significantly affect growth rates ($F_{9,\ 37} = 0.85$, $P = 0.57$; Fig. 2F), but the change in developmental rate was nearly statistically significant ($F_{9,\ 37} = 1.9$, $P = 0.08$; Fig. 2F).

Two factors, dissolved oxygen and ammonium, were included in the best model to predict dry body mass in 1997 (Fig. 3, Table 1). Days since

hatching and dissolved oxygen were included in the model to predict dry body mass in 1998 (Table 1). Although dissolved oxygen was the only factor included in the predictive models for both years, it was not the most important variable in both years, and the direction of the effect of dissolved oxygen on dry body mass was inconsistent. Tadpole developmental stage was best predicted by days since hatching and dissolved oxygen in 1997 (Fig. 3, Table 1). In 1998, days since hatching, ammonium, and water temperature were included in the predictive model for developmental stage (Table 1). Factors which explained the most variation in the predictive models for dry body mass and developmental stage were variable. Days since hatching and dissolved oxygen were included in the models most often followed by ammonium. Overall, growth and development of tadpoles were more variable in 1998 than in 1997 (dry body mass, 1997: C.V. = 58.06, 1998: C.V. = 89.02, developmental stage, 1997: C.V. = 4.82, 1998: C.V. = 10.96).

Larval Period.—In 1996, tadpoles from bison wallows generally were between Stage 38 and 42 when all wallows had dried (i.e., 26 days after egg deposition). Consequently, we collected 12 tadpoles from drying wallows and allowed them to complete their metamorphosis in 2-liter bottles filled with dechlorinated water and placed under ambient conditions of the environment. All tadpoles completed metamorphosis within three days of being collected, for a total larval period of 29 days. We did not observe any frogs that emerged from wet wallows or see any metamorphs around wallows after drying in 1996. In both 1997 and 1998, we did not observe any tadpoles that had developed beyond Stage 25 when the wallows dried.

The average hydroperiod of intermittent streams was six times longer than the average hydroperiod in bison wallows. Despite a mean hydroperiod of 96 (± 3.8) days in 1997, we did not observe any metamorphs emerging from intermittent stream sites while they held water. On average, tadpoles were at Stage 33 (± 0.7) at the time that intermittent streams dried. When intermittent streams dried in 1998, tadpoles were, on average, at Stage 33 (± 0.7). However, we observed newly metamorphosed frogs at four of the 10 intermittent stream sites in 1998, although the average hydroperiod of intermittent streams was less than in the previous year (61 ± 3.0 days). Variation in larval period among years and sites may be partly caused by differences in mean water temperature (1997: 11.4 ± 0.9°C; 1998: 17.7 ± 0.6°C). Maximum developmental stage at the time the streams dried was not correlated with number of days since first hatching in either year (1997: $r = 0.46$, df = 4, $P = 0.44$; 1998: $r = 0.26$, df = 9, $P = 0.51$). We were unable to determine whether this lack of correlation was caused by individual tadpoles failing to continue to develop or high turnover of tadpoles (either from predation or drift).

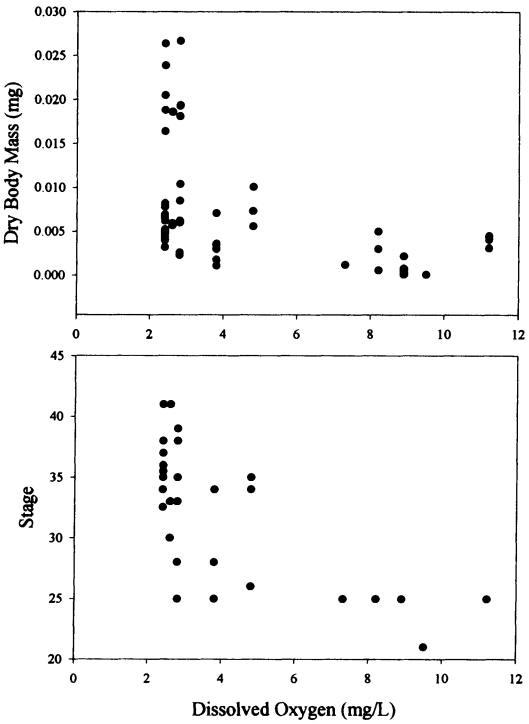

FIG. 3. The relationship between dry body mass and Gosner developmental stage and dissolved oxygen for Western Chorus Frog (*Pseudacris triseriata*) tadpoles collected from intermittent streams in 1997 on Konza Prairie Biological Station, Kansas.

Laboratory Study

Growth and Development of Tadpoles.—Developmental rates of tadpoles differed among treatments throughout the experiment ($F_{2, 23} = 1066$, $P < 0.0001$; Fig. 4). Because interactions between treatments and habitat of origin of tadpoles were not significant ($P > 0.05$), data were pooled across habitat of origin to examine treatment effects. Tadpoles in the high pH treatment were significantly less developed than tadpoles in the control only on Day 19 ($t = 3.47$, df = 22, $P = 0.0021$). Tadpoles in the high ammonium treatment differed marginally significantly from the control on Day 19 ($t = 2.00$, df = 22, $P = 0.05$).

By Day 27, all developmental stages of tadpoles across treatments were similar. It is possible that the lack of significant differences among treatments in developmental stage by Day 27 may have been caused by small sample size. To test this possibility, we subsampled the larger metamorphic dataset. Five datapoints were

TABLE 1. Multiple regression predictive models for dry body mass (milligrams) and developmental stage (Gosner) of Western Chorus Frog (*Pseudacris triseriata*) tadpoles in streams on Konza Prairie Biological Station for 1997 and 1998. Independent variables included in the models were dissolved oxygen (mg/L), ammonium (mg/L), days since hatching (d), and water temperature (°C).

	Variable	df	R^2	P	Beta	SE	F
Dry body mass							
1997	Intercept			0.0005	0.02	0.0029	46.96
	Dissolved oxygen		0.70	0.005	−0.002	0.0004	31.27
	Ammonium		0.15	0.05	−0.00003	0.00001	5.74
	Model	8	0.85	0.0037			16.48
1998	Intercept			0.01	−0.0077	0.003	7.08
	Days since hatching		0.51	0.0001	0.0007	0.0001	41.44
	Dissolved oxygen		0.03	0.1171	0.0005	0.0002	2.57
	Model	42	0.54	0.0001			23.41
Developmental stage							
1997	Intercept			0.0021	28.55	5.546	26.50
	Days since hatching		0.01	0.09	1.103	0.548	4.05
	Dissolved oxygen		0.96	0.0001	−1.215	0.326	190.19
	Model	8	0.98	0.0001			138.51
1998	Intercept			0.0001	21.31	1.87	130.00
	Days since hatching		0.46	0.0001	0.39	0.09	19.58
	Ammonium		0.04	0.0819	−0.025	0.014	3.10
	Water temperature		0.03	0.1428	0.151	0.1	2.24
	Model	42	0.53	0.0001			14.44

selected randomly from each treatment and analyzed by using a two-way ANOVA with a completely randomized block design (as was done originally with the whole metamorphic dataset). In each case of subsampling and analyses, we still found a significant treatment by habitat of origin interaction. Thus, it appears that our sample size of five from each treatment was large enough to detect differences in growth and development among treatments.

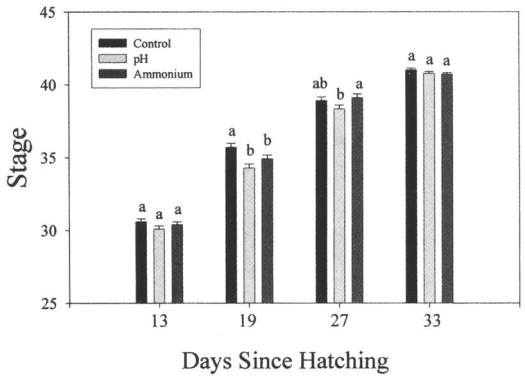

FIG. 4. Effects of high ammonium and high pH on development (Gosner stage) of *Pseudacris triseriata* collected from bison wallows and intermittent streams on Konza Prairie Biological Station, Kansas. Five tadpoles from wallows and five tadpoles from streams from each treatment were selected randomly and staged each week during the larval period. Bars represent means with one standard error. Lowercase letters that are not the same indicate statistically significant differences among the means ($P < 0.05$; least squared means multiple-contrast test).

SVL did not differ between tadpoles from wallows and tadpoles from streams during the larval period ($F_{1, 23} = 0.37$ $P = 0.55$). No differences in SVL of tadpoles were observed between treatments and the control.

Larval Period.—The effects of the experimental abiotic treatments on larval period depended on habitat of origin (treatment by habitat of origin interaction: $F_{2, 81} = 5.46$, $P = 0.006$; Fig. 5). As hypothesized for the high ammonium treatment, tadpoles from streams had significantly shorter larval periods than tadpoles from wallows. In contrast, in the high pH treatment, tadpoles from wallows metamorphosed significantly faster than tadpoles from streams. Overall, tadpoles from wallows in the control group had the shortest larval periods. Within the control group, tadpoles from wallows tended to metamorphose in fewer days than tadpoles from streams, but this response only approached significance ($P = 0.07$).

Size at Metamorphosis.—Because size of tadpoles at metamorphosis was not affected by an interaction between treatments and habitat of origin, data were pooled across habitat of origin (dry body mass: $F_{2, 78} = 1.50$, $P = 0.23$). Tadpoles in the control group were significantly larger at metamorphosis as indexed by dry body mass than tadpoles in all other treatments ($F_{2, 78} = 7.53$, $P = 0.0011$). Tadpoles with shorter larval periods emerged with higher dry body mass than

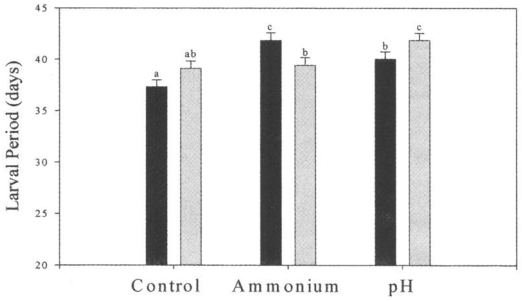

FIG. 5. Effect of high ammonium and high pH on length of larval period (number of days from hatching to metamorphosis) of *Pseudacris triseriata* tadpoles collected from bison wallows (dark bars) and intermittent streams (gray bars) on Konza Prairie Biological Station, Kansas. Bars represent means with one standard error. Different lowercase letters indicate statistically significant differences among means ($P < 0.05$; least-squared means multiple-contrast test).

tadpoles that delayed metamorphosis (Fig. 6; $r = -0.54$, df = 75, $P = 0.0001$). In contrast to dry body mass, length of larval period did not affect SVL (Fig. 6; $r = 0.23$, df = 75, $P = 0.12$).

DISCUSSION

We expected that at least a subset of abiotic factors would change predictably with habitat desiccation in both bison wallows and intermittent streams. In bison wallows, pH increased gradually as they dried, whereas in intermittent streams, ammonium levels increased with decreases in both stream depth and dissolved oxygen. Other studies of temporary aquatic habitats have reported several abiotic factors that change in predictable ways with pool desiccation (Black, 1976; Wright, 1985; Williams, 1987), but these can vary with the type of aquatic habitat. Wallows and streams are positioned in and drain different aspects of the same landscape. Wallows are isolated habitats from the time they fill, but intermittent stream sites do not become isolated until flow stops. Variation in these factors may be sufficient to account for the observed abiotic differences between bison wallows and intermittent streams.

Days since hatching, levels of dissolved oxygen, concentration of ammonium, and temperature of water affected the growth and development of tadpoles in streams and wallows in the prairie. Ammonium was the only abiotic factor that changed significantly with changes in growth and developmental rates of the tadpoles. In 1997, increased levels of ammonium were correlated with slowed growth of tadpoles and in 1998, increased levels of ammonium were associated with decreased developmental rates in tadpoles. The relationship between dissolved oxygen levels and growth and development of

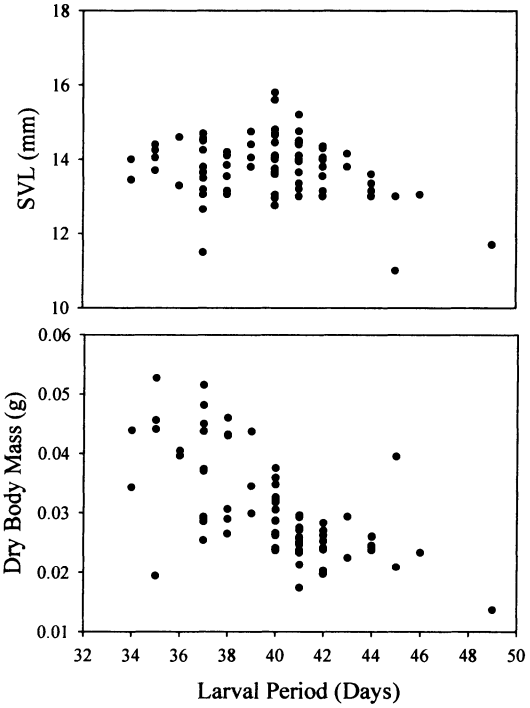

FIG. 6. The relationship between size (snout–vent length [SVL] and dry body mass) and length of the larval period (number of days from hatching to metamorphosis) in *Pseudacris triseriata* tadpoles collected from bison wallows and intermittent streams on Konza Prairie Biological Station, Kansas. SVL and dry body mass at metamorphosis were recorded for each tadpole and pooled from all treatments.

tadpoles was less clear, which is why we chose ammonium for our laboratory experiments. In 1997, dry body mass of tadpoles increased with low levels of dissolved oxygen, but in 1998, the reverse was true.

Water temperature increased throughout the sampling period in both wallows and intermittent streams in 1997 and 1998. Increased temperatures (unless they reach stressful levels: Skelly and Freidenburg, 2000) likely increased the growth and developmental rates of tadpoles (Duellman and Trueb, 1986) and contributed to the variation in length of larval period of tadpoles and possibly their size at metamorphosis (Smith-Gill and Berven, 1979; Newman, 1989; Hayes et al., 1993). Regardless of other cues present in the larval environment, ambient temperatures may set constraints on how quickly tadpoles can reach the minimum size or stage necessary for metamorphosis. This constraint may explain why frogs emerged from intermittent streams in 1998 but not in 1997 when the mean water temperature was lower. Other factors, such as tadpole density and food availability, could have con-

strained growth and development (Newman, 1994; Walls, 1998; Glennemeier and Denver, 2002) but were not measured in the field.

In the high ammonium treatment, tadpoles from streams had significantly shorter larval periods than did tadpoles from wallows. In contrast, tadpoles from wallows metamorphosed significantly faster in the high pH treatment than tadpoles from streams. Differences in response between tadpoles collected from wallows and from streams to increased ammonium and pH correspond to factors they would encounter in the habitat of origin. These results suggest that either cues originating from natal habitat, or genetic differences between populations that use these different habitats, have an influence on the response of tadpoles to changes in some abiotic factors. Embryos were allowed to complete development in their natal habitat before they were collected for the experiments (within 24 h after hatching). The observed phenotypic responses of tadpoles to different experimental environments may be the result of embryonic exposure in the natal habitat. Maternal effects also may contribute to variation in tadpole growth and development (Skelly and Freidenburg, 2000; Loman, 2002; Pakkasmaa et al., 2003; Sommer and Pearman, 2003).

If genetic differences occurred, it would suggest a lack of gene flow between *P. triseriata* breeding in bison wallows and those breeding in intermittent streams. A genetic difference seems unlikely given the close proximity of these breeding sites and the stochastic nature of bison wallows as an aquatic habitat. Despite the low likelihood, a few genetic studies have shown that even when migration occurs between close populations, local selection pressure can limit the reproductive success of immigrants resulting in genetic divergence between populations (Hendry et al., 2000; Skelly and Freidenburg, 2000; Relyea, 2002). However, examination of long-term climatic records from the Konza Prairie area demonstrated that the conditions necessary for completion of metamorphosis in bison wallows only occurred in about 18 of the 82 years examined (Gerlanc and Kaufman, 2003). If this model provides an accurate estimate of the frequency of favorable breeding conditions in bison wallows, alternate breeding sites would be important to long-term maintenance of these populations of *P. triseriata*.

Tadpoles in high ammonium and high pH treatments did not complete metamorphosis before tadpoles in the control group. Therefore, we have to reject our hypothesis that these two abiotic factors serve as cue for an adaptive increase in developmental rate. Changes in pH occur gradually in the natural habitat of the experimental tadpoles; hence, our results might have been different if we had changed this factor slowly. Ammonium levels in streams increased rapidly at the end of the hydroperiod; therefore, a spike in the level of ammonium was appropriate. However, application at a later stage in development might have served as a more effective mimic of a developmental cue that tadpoles experience in streams.

Tadpoles in the high pH and high ammonium treatments developed more slowly than tadpoles in the control early in the experiment. Differences in early developmental rates may be in part caused by stress caused to the tadpoles from exposure to experimental levels of treatment early in their development. The stage that we chose to introduce the treatments to the tadpoles was based on stages used in previous studies (Alford and Harris, 1988; Skelly and Werner, 1990; Hensley, 1993). Our intent was to start the treatments at a stage when tadpoles would be able to respond to differences in environmental cues.

Abiotic factors may act as indicators of habitat desiccation in the field. Under conditions present in the field, these factors may act alone or work in conjunction, or in opposition, to affect tadpole growth and development (Denver et al., 1998). Future laboratory experiments should alter levels of the abiotic factor gradually to simulate natural conditions, introduce changes in levels of abiotic factors at different developmental stages, and test for interactions among abiotic factors to clarify the role that the abiotic environment plays in tadpole growth and development. Transplant experiments, including laboratory experiments which use eggs laid in the laboratory that are never exposed to the natal habitat or eggs from a laboratory colony where individuals are several generations removed from natural habitats, and genetic analyses on a population level are all possible ways of understanding further the relationship between selection in the natal habitat and the response of tadpoles to proximate abiotic factors.

Our study suggests that changes in abiotic factors throughout the larval period caused differences in growth and developmental rates of *P. triseriata*. We also determined that abiotic factors, which changed during the larval period, differed between two habitats despite their proximity in the prairie landscape and that natal habitat may determine how tadpoles respond to changes in abiotic factors. Our research highlights the benefits of studying larval growth and development under both natural and laboratory conditions. Questions regarding the constancy of abiotic changes in streams and in wallows among sites and among years only can be answered by further study of this system.

Future studies on amphibian metamorphosis should consider how changes in water chemistry

over time might affect tadpole growth and development in conjunction with the other factors being studied and take into consideration potential abiotic differences among habitat types used by populations of interest. Assessing amphibian populations as to where they fit on the continuum from phenotypic plasticity to local adaptation not only has implications for understanding contemporary evolution but might also lead to an understanding of the potential for amphibians to adapt to continued environmental degradation resulting from habitat loss, urban development and global climate change.

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