

Are Tadpoles of the Illinois Chorus Frog (*Pseudacris streckeri illinoensis*) Cannibalistic?

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ABSTRACT

Little is known about the ecology of Illinois chorus frog (*Pseudacris streckeri illinoensis*) tadpoles. We reared Illinois chorus frog tadpoles from eggs and observed evidence that this species' tadpoles are cannibalistic. This behavior appears to be facultative based on increased mortality rates of tadpoles raised on low protein rations compared to tadpoles raised on high protein rations. Additionally, a large tadpole was observed carrying a small living tadpole in its mouth. Despite netting this individual and handling during photography, it refused to release the small individual. Photographic evidence that Illinois chorus frog larvae of identical ages fed identical rations in identical housing conditions show differential development reminiscent of large and small larval morphotypes combined with the tenacity with which the large larvae maintained its grip on the small one provide evidence that some of these larvae develop into cannibalistic morphotypes under appropriate conditions.

Key Words: Illinois chorus frog, *Pseudacris streckeri illinoensis*, tadpoles, cannibalism, Arkansas

INTRODUCTION

Evolutionarily strategies (ESS), conceptually derived from Game Theory, are those sets of rules of behavior that when adopted by a certain proportion of individuals in the

population cannot be replaced by any alternative strategy (Dawkins, 1980). Cannibalism is one of the more difficult ESS's for ecologists to understand; yet, it remains present throughout the animal kingdom and occurs most frequently under conditions of high density and food limitation (Crump, 1983). In many species the consequences of cannibalism include population regulation and alteration of age class structure resulting in lowered intraspecific competition (Crump, 1983). *Scaphiopus* may incur reduced individual survivorship of cannibalistic morphs through accumulation of toxins and parasites (Pfenig et al., 1991). Cannibalism may reduce an individual's inclusive fitness through kin selection if an individual feeds on its siblings (Polis, 1981). It may also reduce kin competition through differential utilization of prey resources between cannibalistic and non-cannibalistic siblings, potentially resulting in higher survivorship of relatives from the same clutch (Crump, 1983).

Cannibalism involving anuran tadpoles is well documented (Hoff et al., 1999) but is most common in species from xeric, ephemeral habitats (Crump, 1983) and tropical species that breed arboreally. Most of these cases involve oophagy (Crump, 1983); however, tadpole-tadpole cannibalism also occurs and typically involves predation on different size classes or life stages (Hoff et al., 1999). Tadpole cannibalism is most common in spadefoot toads (*Scaphiopus*), where cannibalistic and herbivorous morphotypes are present (Hoff et al., 1999). Other species participating in apparently facultative cannibalism include wood frogs (*Rana sylvatica*) (Bleakney, 1958), northern leopard frogs (*Rana pipiens*) (Salthe and Mecham, 1974), and various tree frogs (Hylidae) (Hoff et al., 1999).

The Illinois chorus frog (*Pseudacris streckeri illinoensis*) is an unusual hylid with a range restricted to sand prairies of northeastern Arkansas, southeastern Missouri, and southeastern and central Illinois (Brown and Rose, 1988; Conant and Collins, 1998). This species leads a highly fossorial lifestyle and is seldom encountered above ground outside of the 1 - 2 week long breeding season (Brown et al., 1972). It is capable of subterranean feeding, digging forward with its forelimbs and eating invertebrate prey as they are encountered (Brown, 1978). The forearms may be utilized to capture subterranean prey based on observations of surface feeding by McCallum and Trauth (*In Press*). The breeding season extends from late February through early March and is characterized as both explosive and sporadic (Brown and Brown, 1973). Defensive posturing (McCallum et al., *In press*), post-metamorphic growth and survivorship (Tucker, 2000), and reproductive biology (Butterfield, 1988, Butterfield et al., 1989) of the Illinois chorus frog have been described, but most aspects of this species natural history, especially its larval ecology, are chiefly unknown. During an attempt to understand components of the Illinois chorus frog's larval nutritional requirements we began to observe evidence of cannibalistic relationships between large and small larval morphologies as described below.

MATERIALS AND METHODS

On 24 February 2000, three male and three female *Pseudacris streckeri illinoensis* were collected while in amplexus from a breeding chorus located in Clay County, Arkansas. The three pairs were housed communally in a 15 x 30 x 15 cm plastic box with about 4 cm of dechlorinated tap water. The following morning (25 February 2000) several small clutches of eggs were present. The total number of eggs was counted, and then they were incubated at 20°C in the same boxes where they had been laid. For seven days following

hatching the tadpoles were allowed to remain with and feed on their egg masses. Groups of five tadpoles then were distributed into each of 15 plastic boxes filled with 3 L of dechlorinated water. Beginning 7 March 2000, groups of four boxes of five tadpoles were placed on each of five soybean meal (sbm)/fescue diets as follows: 100% soybean meal, 75/25, 50/50, 25/75, 100% fescue. Tadpoles were fed 0.25 g of each diet per box per day. After the first week, tadpoles were provided with minimal surplus of each diet so that only a few grains remained at the next feeding. On 17 April 2000, The 15 containers of *P. s. illinoensis* tadpoles were transferred to larger 10 x 60 x 90 cm plastic boxes in order to maintain water quality with the greater volumes of food and waste products associated with the growing larvae. Wood frog (*Rana sylvatica*) and southern leopard frog (*Rana sphenoccephala*) tadpoles were treated identically as controls. Minitab 3.0 was used to calculate regression analyses.

RESULTS

A total of 170 eggs was laid (approximately 57 eggs per female). The first free-swimming *Pseudacris streckeri illinoensis* larvae were observed 1 March 2000. By 4 March 2000, 112 larvae free-swimming were present. This represented a 65.9% survivorship from eggs to free-swimming larvae. The survivorship of *P. s. illinoensis* in each treatment is shown in Table 1. The survivorship of Illinois chorus frog tadpoles on each diet appeared to drop as both the soybean component was reduced and as length of time on that ration increased ($r^2_{\text{pred}} = 89.16\%$, $P = 0.000$). Mortality rates of Illinois chorus frog tadpoles did not appear substantially different between treatments as of 2000 March 28 ($r^2 = 48.9\%$, $P = 0.189$). By 2000 April 3 survivorship was showing a positive relationship with an increasing sbm component ($r^2 = 82.7\%$, $P = 0.032$). Some tadpoles appeared slightly larger than others at this time, but the data were not quantified. By the 37th day of the study there was no longer a definite linear relationship between sbm component and mortality (ANOVA: $F_{1,3} = 3.375$, $P = 0.164$) and by the 51st day there was no association between diet and mortality ($r^2 = 0.0\%$, $P = 1.0$).

While transferring tadpoles to larger quarters, one large tadpole was observed carrying a small one in its mouth (Fig. 1). In this photo you can distinctly see the size difference between the two morphs of the same age and fed the same diet. The small larvae could be observed thrashing weakly in the grasp of the larger one. The large morph's grasp on its smaller victim's tail was tenacious enough that it did not release its prey, even after being pursued by the investigators and transferred to a small jar where it was photographed. Despite the obvious reductions in experimental populations for this study (100% mortality), few remains of Illinois chorus frog larval body parts were noticeable. Some remnants of vertebrae, skulls, and skin were all that usually remained. Conversely, dead wood frog (*R. sylvatica*) and leopard frog (*R. sphenoccephala*) tadpoles were usually recovered intact. Wood frog (*R. sylvatica*) experimental populations dropped from 75 to 56 tadpoles (26.4% mortality), and southern leopard frog (*R. sphenoccephala*) populations dropped from 75 to 51 tadpoles (32% mortality) while each was under the same housing and diet constraints.

DISCUSSION

Tadpoles on high protein rations persisted longer than those fed low protein diets (Table 1) giving the initial appearance that tadpoles were dying from protein deprivation. Soybean meal is usually around 44% protein, whereas fescue commonly contains only around 9% (Jurgens, 1988). Consequently our treatments of 100%, 75%, 50%, 25%, and 0% sbm can be mathematically estimated using the Pearson square technique (Jurgens, 1988) as 44%, 35%, 27%, 18%, and 9% protein respectively, revealing that protein content of the diets was more limiting as the sbm fraction was reduced. Since tadpoles of the other species had mortality rates around 30% under the same conditions, the added mortality in Illinois chorus frog tadpole colonies might have been contributed by cannibalism or an unusually high protein requirement by these tadpoles. Until further diet studies on protein requirements for this species are conducted, we have little evidence of an unusual protein need in Illinois chorus frog tadpoles.

The last tadpoles alive in all treatments were the large morphotypes, which ceased to grow or metamorphose once conspecifics were eliminated. Because we did observe cannibalism and because large tadpoles with plenty of food ceased to grow or develop once potential prey was eliminated, it seems probable that the added mortality between treatment groups was due at least in part to this behavior and not entirely to protein requirements by these larvae. Starrett (1960) has provided evidence that in other anurans expression of tadpole cannibalism is often facultatively expressed in response to food abundance. If this is the case in the Illinois chorus frog we might infer that its protein requirement triggers cannibalism facultatively when this nutrient is in low supply.

Cannibalism may be an important trait for the persistence of xerically-adapted species (Crump, 1983), such as the Illinois chorus frog. Ponds where these tadpoles develop are extremely susceptible to drying and are often short-lived. Spawning occurs in flooded agronomic fields that are primarily composed of sand. Water quickly percolates from the surface during drought conditions (such as experienced in Arkansas from 1999-2000). Eggs are laid during heavy rains in the spring without the benefit of prior colonization of these ponds by plankton and algae. Tadpoles remained near and appeared to feed on their egg masses; cannibalism was not observed during this time. Such behavior may allow time for the pond microcosm to become established.

Based on this evidence, cannibalism may begin expression by tadpoles between day 28 and 54 of development. Treatment associated mortality was not observed prior to this (Table 1). By the 54th day, however, survivorship was no longer associated with feeding regime suggesting that mortality was resulting from cannibalism in all treatment groups by this time, and not diet. If their protein requirement was exceeding that provided by all the ration formulas by the 54th day, tadpoles may have developed into cannibalistic morphs and quickly eaten the available herbivorous tadpoles. This is supported by the reduction in high protein treatments during the latter part of the study.

Growth rate differences (but not mortality differences) were observed under these treatments for other species (unpublished data), suggesting that cannibalism appeared during this time to enhance dietary protein and that this macronutrient's deficiency was not causing direct mortality.

Cannibalism is an important strategy for resource allocation in any population. Under ideal circumstances natural selection should eliminate larval phenotypes that feed on foods other than conspecifics. Such behavior maximizes reproductive potential through kin selection as well as through the individual's personal reproductive potential. Without this added source of predation only intraspecific competitive exclusion would persist (i.e., something that is usually low when considering planktonic food sources in ponds). This would normally maximize the probability that any individual will survive to reproduce. Illinois chorus frog tadpoles do not live in the ideal situations described above. Their habitat is highly susceptible to desiccation and is low in extended productivity (Cole, 1988) due to the permeability and inert qualities of the sandy substrate as well as short-lived nature of their breeding ponds. Such xeric, ephemeral habitats require their inhabitants to possess unique adaptations that provide maximal benefits to the individual's reproductive capacity under these circumstances.

Cannibalism may provide an insurance policy for Illinois chorus frog larvae by allowing them to feed on conspecifics (and probably small plankton as well) ensuring that food will not become limiting before metamorphosis is complete.

The highest risk to survival of tadpoles from sand prairies is probably the evaporation of their breeding pools. The persistence of both morphotypes could ensure that some recruitment occurs every year in which breeding pools last long enough for metamorphosis to transpire. Individuals that do not produce both morphotypes would be under severe selective pressure and would be capable of producing viable young only during those few years in which ponds do last long enough; the ideal conditions are present for their prey type. Our data provide photographic evidence that Illinois chorus frog larvae of identical ages fed identical rations in identical housing conditions show differential development reminiscent of large and small larval morphotypes. Description of the tenacity with which the large tadpole retained its grasp on the smaller one is provided and not expected from a tadpole that does not hold adaptations specifically for such behavior. Further circumstantial evidence based on initial changes in survivorship explainable by protein changes in the diet, followed by final balance in survivorship that is not explainable by this factor suggest that cannibalism was eventually occurring in all treatments. Finally, the recovery of only body parts in Illinois chorus frog housing, but entire tadpoles from chambers of other species, suggests that Illinois chorus frog larvae were at least more likely to feed on the dead/dying larvae than other species regardless of this species cannibalistic tendencies. When this evidence is combined, it substantiates the theory that the Illinois chorus frog is capable of developing cannibalistic larval morphotypes in parts of its range.

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Table 1. Survivorship of Illinois chorus frog tadpoles on each of five diets. Percentages are the percent of soybean mean in each diet, and the numbers in each column represent the number of tadpoles present on that date.

Date	100%	75%	50%	25%	0%	TOTAL
March 7	20	20	20	20	20	100
March 28	14	16	9	13	8	60
April 3	13	15	9	8	5	50
April 17	5	7	1	3	1	17
May 17	1	0	0	0	0	1

Figure 1. Cannibalistic morph grasping the tail of a smaller tadpole of Illinois chorus frog (*Pseudacris streckeri illinoensis*). The small morphotype's tail is extending out of the mouth of the large tadpole (depicted above the drawn line).

