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Carnivorous Spadefoot (*Spea bombifrons* Cope) Tadpoles and Fairy Shrimp in Western Iowa

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Amphibian larval polymorphisms, rarely found in the Midwest, are more common in arid western regions. We have discovered that Plains spadefoot toad, *Spea bombifrons* Cope, tadpoles occur as carnivorous and omnivorous morphological forms in flooded soybean and corn fields on the Missouri River flood plain of western Iowa. Carnivores have longer snouts, larger beaks with an upper cusp and lower notch, shorter intestines with fewer loops than the omnivores, and they feed on fairy shrimp. A similar polymorphism in *Spea multiplicata* Cope enhances survival in the desert because the carnivore develops faster after consuming fairy shrimp and is able to metamorphose in rapidly drying ponds. However, the omnivore develops slower in deeper ponds, stores more fat and has better postmetamorphic success. Fairy shrimp ingestion triggers development of the *S. multiplicata* carnivores, but whether this is also true for *S. bomifrons* remains to be seen. Distributions and abundance of both carnivorous *S. bombifrons* tadpoles and fairy shrimp need to be determined across the Great Plains and in Iowa.

INDEX DESCRIPTORS: spadefoot, tadpoles, fairy shrimp

Polymorphic spadefoot tadpoles are thought to be extremely rare in the Midwest (Whiteman and Howard 1994, 1997), but are common in the desert southwest and west. Tadpole trophic morphotypes with different feeding habits and diets have been observed in three species of spadefoot toads *Spea multiplicata, S. hammondii* and *S. bombifrons* from Oklahoma, New Mexico, Arizona, Colorado and South Dakota (Bragg 1941, 1957, 1964, Orton 1954, Pfennig 1990 and 1992a and b, Pomeroy 1981) which suggests that polymorphism is adaptive for life in ephemeral ponds associated with arid climates.

The most thoroughly studied polymorphism occurs in *S. multiplicata* in which three tadpole morphotypes, an omnivore, carnivore, and intermediate, have been described (Pfennig 1990, 1992a, and Pomeroy 1981). The omnivorous morph is best suited to longer-lived ephemeral ponds, while the carnivores develop faster and metamorphose at an earlier age, allowing them to succeed better in rapidly drying ponds. The typical omnivore develops more slowly, feeds on algae and detritus, stores more fat, and has a smooth beak and long gut (Pomeroy 1981). The rarer, carnivorous morph is predatory and feeds on fairy shrimp and smaller tadpoles. It has an elongated snout, wider head, hypertrophied jaw muscles, and powerful keratinized beaks with an upper cusp which fits into a notch on the lower beak. It has the typically shorter gut associated with carnivory. Intermediate tadpoles are transitional between the other two types (Pomeroy 1981; Pfennig 1990).

Polymorphic *S. bombifrons* tadpoles have been studied less frequently. They occur as three types, I, II, and III (Bragg and Bragg 1959) roughly corresponding to the omnivore, intermediate, and carnivore of *S. multiplicata,* respectively. Different dietary signals may trigger morph development in *S. bombifrons* and *multiplicata.* Fairy shrimp ingestion is the trigger in *S. multiplicata* (Pfennig 1992a), but the trigger has not been determined for *S. bombifrons.* Field observations led Bragg to describe the type III tadpole as a predaceous cannibal, and dependence on fairy shrimp for development of the cannibal morphology is not known (Bragg and Bragg 1959; Bragg 1964). The influence of fairy shrimp on morphogenesis in this species needs to be clarified.

The objective of this paper is to report on the presence of at least two morphologically distinguishable forms of *S. bombifrons* tadpoles and the occurrence of fairy shrimp in ephemeral floodplain ponds in western Iowa.

METHODS

During the summers of 1994 and 1995, we found flat-headed appearing plains spadefoot tadpoles in one pond each summer, while other ponds contained typical round-bodied tadpoles. We collected tadpoles of each type during 1995, made behavioral observations in captivity, and compared several morphological features of the two types to determine if the two differed behaviorally and morphologically.

Collection and Behavioral Observations

Round and flat-headed tadpoles were seined and netted from two different sites in Lakeport Township of western Woodbury County. Round-bodied tadpoles were taken from a pond with no fairy shrimp and flat-headed tadpoles were collected from a pond with abundant fairy shrimp. Fairy shrimp were also collected and preserved for identification. The tadpoles' behavior toward fairy shrimp was observed in aquaria in the laboratory.

To determine if the flat-headed tadpoles differed morphologically from the round-bodied tadpoles in the same characteristics as described for *S. multiplicata* carnivores and omnivores, we measured and compared ten characters of twenty representative individuals from each pond. The individuals chosen were approximately the same size and age (19–20 days old). Age was estimated from the observed breeding date.

We weighed the animals and determined their developmental stages by two staging methods (Gosner 1960; Taylor and Kollros

1946). Keratinized mouthparts were examined under a dissecting microscope and each tadpole's beak morphotype was recorded. A carnivorous beak was defined as being thick with a median cusp on the upper beak which fit into a notch on the lower beak. Omnivorous beaks were thinner, smoother and lacked the cusp and notch. Vernier callipers were used to measure total length, snout-vent length, snout length (tip of snout to mid-eye distance), head width, orbitohyoideus muscle width, tail muscle height, and total tail height. All measurements were made at the structure's widest or tallest point. Tadpoles were preserved in 70% ethanol, and we later counted the number of intestinal coils and measured gut lengths. Gut length was the straight line distance from the anterior manicotto to the cloaca (Pfennig 1992a). Intestinal contents were microscopically examined and identified. Means of morphological measurements were compared by t-tests, and statistical significance was determined by the sequential Bonferroni technique (Holmes 1979).

RESULTS

Spadefoot Breeding Sites

We found spadefoot tadpoles in 21 ephemeral ponds in Lakeport and Fairview Townships in Woodbury and Monona Counties during the summers of 1994 and 95. The ponds are on the Missouri River flood plain which is extensively planted in corn or soybeans (Fig. 1a). The area is relatively dry and many farms are irrigated. Spadefoot tadpole sites are found in flooded fields and adjacent roadside ditches after heavy rains. These ponds are shallow, typically under 60 cm in depth. The water is generally turbid, especially when the tadpoles are abundant because they stir up the mud on the bottom. The ponds dry up rapidly; they usually don't hold water throughout the summer unless several heavy rains occur. Water temperatures often surpass 32°C. Little aquatic vegetation is associated with the pond. Many of the sites have been planted in row crops prior to flooding or are disced after they dry up.

Behavioral Observations

In 1994, we found tadpoles with broad, flat heads in one of our study sites (Fig. 1c). Typically the tadpoles in other ponds that year had rounder bodies and heads (Fig. 1b). The flat-headed tadpoles were common in this pond as were fairy shrimp. The tadpoles fed voraciously on fairy shrimp in the collecting bucket and later in aquaria in the lab. This behavior could best be described as a feeding frenzy. In fact few fairy shrimp made it back to the lab if the flat-headed tadpoles were in the same bucket with them. The round-bodied tadpoles would nibble on the fairy shrimp, but did not attack them aggressively like the flat-headed tadpoles.

Morphometric Comparisons

In 1995, another pond containing the flat-headed tadpoles was found. These tadpoles were behavioral carnivores like the flat-headed tadpoles collected the previous year. Tadpoles from this pond were used for morphometric measurement comparisons with round-bodied tadpoles.

Even though the tadpoles were collected from two different ponds, they were about the same age (19 to 20 days old), stage (Gosner stage 35 and Taylor and Kollros stage X for the carnivores versus Gosner stage 36 and Taylor and Kollros stage XI for the omnivores), and size (no significant differences in body weight, total length, or snout vent lengths) (Table 1.). However, they differed in head shape, beak types, tail height, and intestinal size. The carnivores had longer snouts ($p<0.003$). Carnivore jaw muscle widths were not statistically different, even when normalized with snout vent lengths. The orbitohyoideus muscle width/snout vent length ratio was 0.13 for both morphs. Carnivores had larger beaks with serrated edges, a large median tooth on the upper jaw and a notch on the lower jaw. Omnivores had thinner, smoother beaks.

Fig. 1a. An ephemeral pond in Lakeport Township, Woodbury County, Iowa containing plains spadefoot carnivorous morph tadpoles. Fig. 1b. Plains spadefoot omnivorous morph tadpole from Lakeport Township, Woodbury County, Iowa. Fig. 1c. Plains spadefoot carnivorous morph tadpole from Fairview Township, Monona County, Iowa.

Omnivores had deeper or taller tails than carnivores. Total height of the omnivore tail averaged 9.9 mm as compared to 7.8 for the carnivore ($p<0.001$).

Carnivore intestines were reduced in length as compared to the omnivore (169.6 mm vs. 276.3; $p<0.001$). The intestinal length to snout vent length ratio was also lower (8.1 vs. 13.4). The decreased length reflected a reduced number of intestinal coils, 5 as compared to 7 ($p<0.001$).

Examination of intestinal contents revealed that both types of tadpoles had consumed some plant material and soil particles. While

Table 1. Characteristics of Twenty Carnivorous and Omnivorous Tadpoles from Two Sites in Lakeport Township, Woodbury County, Iowa.

CHARACTERISTICS	CARNIVORE MEAN ± S.E.	OMNIVORE MEAN ± S.E.	P
Weight (g)	1.3 ± 0.03	1.4 ± 0.04	0.156
Total length (mm)	45.2 ± 4.2	44.2 ± 5.7	0.245
Snout-vent length (mm)	21.0 ± 0.89	20.6 ± 0.97	0.304
Snout length (mm)	6.6 ± 0.13	5.8 ± 0.21	0.003*
Head width (mm)	11.3 ± 0.47	10.2 ± 0.73	0.017
Orbitohyoideus muscle (mm)	2.8 ± 0.13	2.6 ± 0.06	0.220
OH/SV ratio	0.13 ± 0.00	0.13 ± 0.00	0.270
Tail muscle height (mm)	4.5 ± 0.07	4.1 ± 0.12	0.039
Total tail height (mm)	7.8 ± 0.37	9.8 ± 0.53	<0.001*
Intestine length (mm)	170 ± 7.9	276 ± 15.6	<0.001*
Intestinal coils (number)	5 ± 0.2	7 ± 0.3	<0.001*

*Significant difference, sequential Bonferroni

all carnivores had eaten fairy shrimp, no exoskeletons were found in the omnivores' gut contents.

Fairy shrimp living in the same ephemeral pond with the carnivorous morphs were tentatively identified as belonging to the genus *Streptocephalus,* and we are currently identifying several other fairy shrimp that have been found in ephemeral ponds in the study area.

DISCUSSION

Behavioral observations and morphometric measurements indicate that *S. bombifrons* tadpoles occur as at least two morphological types in Missouri River flood plain ephemeral ponds. The two tadpole types can be distinguished by several of the same characteristics previously described for *S. multiplicata* tadpole morphotypes in Arizona (Pomeroy 1981; Pfennig 1992a). *Spea bombifrons* carnivorous tadpoles have longer snouts, more streamlined tails, and shorter intestines with fewer coils than similar age and developmental stage omnivores from a different pond. Carnivores and omnivores differed in their beaks as has been noted previously by Bragg and Bragg (1959) in *S. bombifrons* tadpoles. We expected the orbitohyoideus muscle width might be significantly larger in the carnivores because carnivorous *S. multiplicata* tadpoles have hypertrophied jaw muscles, but it was not. This could be a species difference in morph characteristics, but our data are preliminary and are limited to carnivorous morphs from a single pond and a single time point in the tadpoles' development. Future research will address this question as well as whether morphological intermediate tadpoles are also present.

The two morphological types of tadpoles behaved differently. Carnivores fed continuously on fairy shrimp even while being transported to the lab. Persons collecting animals in the pond containing carnivores experienced the surprising sensation of tadpoles nibbling their legs, which Bragg (1965) also described. Omnivores ate fairy shrimp in the lab, but may have lacked the opportunity to feed on them in nature. Fairy shrimp were not collected from this particular pond and were not found in the omnivores' intestines. Rather, the omnivores had been feeding on algae and detritus, at least at the time of collection. Because there were no fairy shrimp in the omnivore's pond, no conclusions can be drawn about their food preferences. While we did not observe cannibalism in these particular carnivorous tadpoles, Bragg (1957 and 1964) related cannibalistic behavior to development of the carnivore morphology in *S. bombifrons.* Future research will be directed at understanding the relationship between fairy shrimp, cannibalism and *S. bombifrons* tadpole morphology.

The distribution and abundance of carnivorous tadpoles across the Great Plains and in Iowa should be determined. The carnivores appear to be consistently found in the area of Lakeport Township because we have found them in two consecutive years at two different sites. However, this is the first record of morphologically differentiated *S. bombifrons* carnivorous tadpoles in Iowa or in the neighboring plains states.

Polymorphism, such as the trophic polymorphism of the spadefoot tadpole described here, is common in the desert Southwest, but has rarely been documented in the Midwest (Whiteman and Howard 1997). Possible reasons for the apparent rarity of polymorphic tadpoles in the midwest include: 1) polymorphic larvae may actually be rare because the Midwest lacks suitable habitat and conditions for their occurrence; 2) polymorphic larvae may have disappeared due to factors such as habitat destruction before their occurrence was recorded; and 3) polymorphic tadpoles have been overlooked in distributional studies due to sampling bias in favor of adults.

Some combination of these factors probably explains why these polymorphic *S. bombifrons* tadpoles have not been described previously in Iowa. Spadefoot toads have only been known to occur in Iowa since 1967 (Huggins 1971), and spadefoot surveys have emphasized adults not tadpoles (Christiansen 1981; Christiansen and Mabry, 1985; Mabry 1984; Mabry and Christiansen 1982 and 1991; Farrar and Hey in press). Descriptions of breeding habitats have been of a general nature and tadpole biology has not been studied.

How habitat alteration impacts spadefoot tadpoles and other ephemeral pond residents, like fairy shrimp, remains to be determined. Missouri River channelization has altered the flood plain and agricultural land has increased. Ephemeral wetlands are now located in cultivated farm fields.

The association of desert dwelling spadefoot tadpoles (*S. multiplicata*) with fairy shrimp is significant for reproductive success of this species and possibly also for *S. bombifrons.* Fairy shrimp occupy the shortest lived desert ponds, and when fairy shrimp are abundant tadpoles eat them triggering carnivore morphogenesis (Pomeroy 1981; Pfennig 1989, 1990, 1992 a and b). Carnivores grow larger and metamorphose faster. This allows them to escape the pond before it dries. Omnivores occupying the longer lived ponds are thought to have better postmetamorphic success because they have more time to accumulate fat before metamorphosis. We have yet to determine whether feeding on fairy shrimp triggers carnivore formation in Iowa *S. bombifrons* tadpoles and how important ephemeral ponds containing fairy shrimp are for retaining vigorous spadefoot toad populations.

The finding of fairy shrimp in these ephemeral ponds is significant in addition to their association with spadefoot tadpoles. Little is known about anostracan species occurrence and distribution throughout the state. There is a pond in Dickinson County nick-named "Fairy Shrimp Pond" because of the fairy shrimp found there by Iowa Lakeside Laboratory personnel. But to our knowledge no literature specifically addresses species distributions and habitat preferences in the state.

The Missouri River flood plain ephemeral pond ecosystem is previously undescribed for Iowa, but similar ecosystems have been described in the desert southwest and California (Simovich and Fugate 1992). The western Iowa ephemeral ponds contain predominantly spadefoot tadpoles of different morphologies and fairy shrimp, and the inhabitants of this ecosystem are adapted to life in a chemically and physically unstable environment. Their life cycles must be synchronized to the rapid environmental changes (Belk and Cole 1975).

Ephemeral ponds serve as refugia for these species and are essential to their survival and reproduction. In the future we plan to describe species composition, physical and chemical characteristics of the ponds and to investigate the interrelationships between spadefoot tadpoles and fairy shrimp. We welcome reports of sightings and locations of similar habitats containing fairy shrimp.

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