

Aspects of Cannibalistic Morphs in a Population of *Ambystoma t. tigrinum* Larvae¹

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ABSTRACT: We report growth, body size and diet of typical and cannibalistic larval *Ambystoma tigrinum* morphs. The study population, located in northwestern Iowa (43° 23' N, 95° 11' W), currently represents the first instance of larval cannibalistic morphs in the subspecies *A. t. tigrinum* and the northeastern limit of cannibalistic morphs in the *A. tigrinum* complex. A comparison of food habits of typical larvae in 1980, when the cannibalistic morph was absent, with 1981, when the morph was present, shows no basic differences. In both years a wide variety of prey were ingested with *Daphnia* being most abundant. Because 1981 was a drought year and our study ponds were drying, our data support Collins and Check's (1983) work showing that density, not food, affects the expression of cannibalistic morph traits. Cannibalistic morphs grew much faster than typical larvae. If metamorphosis is size-dependent, cannibalistic morphs should have a higher survivorship under drying-marsh conditions.

INTRODUCTION

Large head size, slender body form and enhanced development of vomerine teeth are among characteristics distinguishing cannibalistic from typical larval morphs in the *Ambystoma tigrinum* (Green) complex (Powers, 1903, 1907; Rose and Armentrout, 1976; Darda, 1982). To date, cannibalistic larval morphs (*sensu* Huxley, 1955) have only been reported from two western subspecies, *A. t. nebulosum* Hallowell and *A. t. mavortium* Baird (Collins *et al.*, 1980). We report here cannibalistic morphs from a population of *A. t. tigrinum* larvae in northwestern Iowa. The primary purpose of the present study is to compare growth, body size and diet between typical morphs collected in 1980 and 1981 and cannibalistic morphs, present only in 1981, to increase the understanding of ecological factors that influence the occurrence of these two forms within a population.

MATERIALS AND METHODS

Larvae were identified as the subspecies *Ambystoma t. tigrinum* based on: (1) adult range and coloration (Conant, 1975); (2) female reproductive behavior, *i.e.*, eggs in clusters of approximately 30-100, and (3) gill-raker counts. Counts made from the anterior surface of the third gill arch of 25 animals (28-68 mm standard snout-vent length) sampled during 1980 and 1981, including typical and cannibalistic morphs, showed \bar{x} = 17.3 gill rakers (range 14-20). See Collins *et al.* (1980: Table 1) for a comparison of these characters in all currently recognized *A. tigrinum* subspecies.

The *Ambystoma t. tigrinum* population we sampled was located at the southern extent

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of the prairie pothole region in northwestern Iowa approximately 1.5 km SE of Iowa Lakeside Laboratory (43° 23' N, 95° 11' W). Two adjacent—and during wet years, connected—semipermanent wetlands, which we call Gull Point Marsh and Marina Marsh, were sampled sequentially (due to initial low numbers of salamanders in Gull Point Marsh and their further depletion due to sampling) in 1980. (For details of locations, sizes, and 1980 vegetation characteristics of these marshes, see Lannoo, 1982: 12-13). In 1981, drier conditions prevailed and Gull Point Marsh could not be sampled. Marina Marsh was sampled but dried in early June.

In this part of Iowa, *Ambystoma t. tigrinum* egg clusters are laid in March or April, shortly after ice melts on the marshes. Larvae hatch within a few days of each other and grow rapidly, metamorphosing in mid- to late July. Larvae do not overwinter. In 1980 larvae were sampled from 27 May, which was ca. 3 weeks after peak hatching activity, to 14 July, when metamorphosis began. In 1981, we sampled from 23 April, the time of most intense hatching activity, to 31 May, shortly before Marina Marsh dried.

During both years larvae were collected individually with a dip net (20 x 40 cm) at night between 2130 and 0100 CDT. Each larva collected was immediately placed in 10% formalin, which killed it without causing it to regurgitate its stomach contents. In the laboratory snout-vent lengths (SVL), head widths (HWID), and wet weights (WT) were measured. Stomach contents of each larva were identified to the nearest practical taxon (using keys by Pennak, 1978, and Merritt and Cummins, 1978) and enumerated. Morphometric data were analyzed using the Statistical Analysis System procedures GLM and ANOVA (Barr *et al.*, 1979) or MINITAB (Ryan *et al.*, 1976). Nonlinear data were transformed to natural logarithms. In 1981 larvae collected before 22 May (before any animals had developed prominent cannibalistic traits) were used in calculating growth and morphometric equations for both cannibal and typical morphs. To compare HWID and WT slopes between these morphs, data were divided by SVL, transformed to natural logarithms and the difference in ratios tested.

RESULTS

The largest larvae collected in 1981 prominently exhibited the classic cannibalistic traits of broad heads, "u-" rather than "v-" shaped snouts, enlarged vomerine teeth, greater numbers of vomerine teeth, and slender bodies (Fig. 1). Some smaller larvae collected in 1981 had better-developed vomerine teeth than equal-sized larvae collected in 1980; however, other morphometric traits were not distinguishing and these smaller animals were conservatively designated typical morphs.

Larvae collected in 1980 exhibited SVLs from 16-79 mm. Growth (SVL) was linear through June, then showed a premetamorphic leveling off in July, when larvae averaged ca. 60 mm SVL (Fig. 2A). In 1981 larvae were collected immediately after hatching and showed an early lag phase in growth (Fig. 2B). In 1981 large typical larvae appeared to be following the 1980 growth trend. It seems reasonable to assume that had Marina Marsh not dried in 1981, a similar linear growth phase followed by a cessation of growth preceding metamorphosis would have occurred. Growth equations from 1981 are given in Table 1A.

Overall trends in HWID and WT data were similar between years (Table 1B,C). For both measurements, the 1980 regression equations had shallower slopes (*i.e.*, lesser rates of increase) and greater y-intercepts than 1981 equations for either typical or cannibalistic morphs. In part this may be due to the smaller larvae collected in 1981. Rates of increase for HWID and WT in 1981 were greater for cannibalistic morphs than for typical larvae (in each case $p > F < 0.01$).

Food habits were similar between typical larvae for the two years (Table 2). In both years typical larvae ate a wide range of prey with *Daphnia* being numerically most important. While there were differences between years in proportions of specific prey groups eaten, overall there were no trends. Cannibalistic morphs tended to eat larger

prey such as crayfish, tadpoles and conspecifics, but also ate zooplankton and aquatic insects. Only five of 10 cannibalistic morphs sampled had *Ambystoma tigrinum* larvae in their stomachs and active cannibalistic individuals tended to be over twice the size of prey larvae.

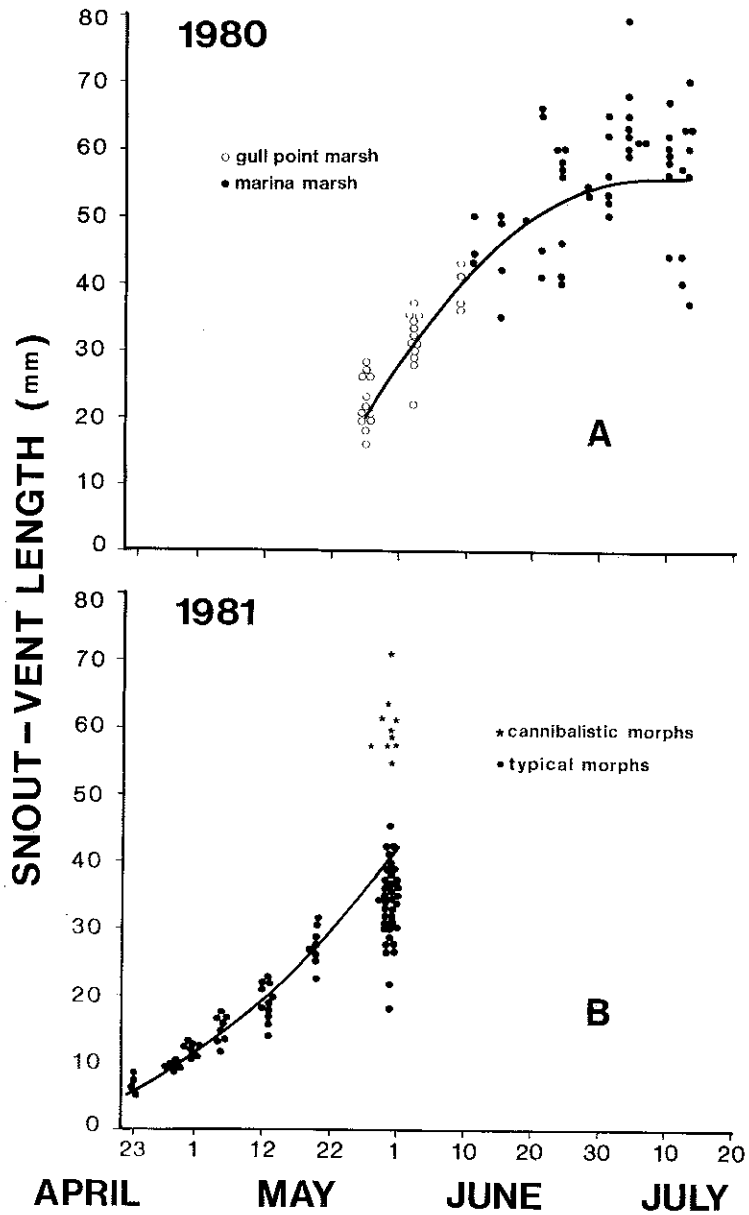


Fig. 1. — A comparison of the dorsal mouth region and head shape of an *Ambystoma t. tigrinum* typical larval morph collected in 1980 (left) with a same-sized (71 mm SVL) cannibalistic morph collected in 1981 (right). Note the prominent vomerine teeth, wider head and "u"-shaped snout of the cannibal

DISCUSSION

We report here the first instance of larval *Ambystoma t. tigrinum* cannibalistic morphs and extend northeasterly the known range of this morph in the *A. tigrinum* complex. Recent attention has been paid to the population dynamics, causes and evolution of cannibalism (Fox, 1975; Polis, 1981; Crump, 1983). Here we treat these subjects for larval *A. tigrinum*.

Like cannibalistic morphs of other species (Polis, 1981), cannibalistic *Ambystoma tigrinum* larvae are the largest animals in a population (Rose and Armentrout, 1976; Pierce *et al.*, 1983). In 1981 we found all larger larvae (SVL > 50 mm) were cannibalistic morphs. Intermediate-sized larvae (30-50 mm SVL) had enhanced vomerine teeth development (Darda, 1982) but showed no other cannibalistic traits. It is possible that intermediate-sized larvae were in initial stages of expressing these traits. The smallest larvae (SVL < 30 mm) did not show any characteristic cannibalistic traits.

For both HWID and WT vs. SVL our cannibalistic morph equations had steeper slopes than equations for typicals, suggesting that HWID and WT were increasing at a greater rate for cannibals. This trend is opposite to that found by Pierce *et al.* (1983). Pierce *et al.* suggest that cannibals have a larger head size throughout their ontogeny. However, their suggestion is based on extrapolations from regressions: There is as yet no direct evidence for this in nature. In our study, animals could not unequivocally be identified as cannibalistic morphs until late in their larval ontogeny.

That cannibal morphs were present in 1981 and not 1980 suggests that environment has an effect in inducing this morph. Whether genetic differences are involved is not known. Pierce *et al.* (1981) suggest, based on allozyme frequencies, that cannibal and typical morphs are genetically different, and experiments by Collins and Cheek (1983) suggest that cannibalism in *Ambystoma t. nebulosum* is a result of the environment

TABLE 1.—A comparison of equations derived from growth and morphometric data from typical morph *Ambystoma tigrinum* larvae collected in 1980 and typical and cannibalistic larval morphs collected in 1981. In A, because date of peak hatching for 1980 is not known, age could not be accurately determined and a growth equation could not be calculated

A.		
Ln Snout-vent length vs. age (days)		
1981		
Typical morphs	$\text{LnSVL} = 1.99 + 0.039 \text{ Age}$	($r^2 = 0.88$)
Cannibalistic morphs	$\text{LnSVL} = 1.77 + 0.056 \text{ Age}$	($r^2 = 0.93$)
B.		
Head width vs. snout-vent length		
1980		
1981		
	$\text{HWID} = 1.79 + 0.26 \text{ SVL}$	($r^2 = 0.96$)
Typical morphs	$\text{HWID} = 0.31 + 0.30 \text{ SVL}$	($r^2 = 0.98$)
Cannibalistic morphs	$\text{HWID} = -0.43 + 0.35 \text{ SVL}$	($r^2 = 0.99$)
C.		
Ln weight vs. Ln snout-vent length		
1980		
1981		
	$\text{LnWT} = -9.0 + 2.78 \text{ LnSVL}$	($r^2 = 0.99$)
Typical morphs	$\text{LnWT} = -10.2 + 3.02 \text{ LnSVL}$	($r^2 = 0.97$)
Cannibalistic morphs	$\text{LnWT} = -10.6 + 3.20 \text{ LnSVL}$	($r^2 = 0.98$)

acting on certain genotypes. In Collins and Cheek's experiments, larval density, not food shortage, stimulated expression of cannibalistic traits. We did not quantify salamander density, but when we sampled Marina Marsh in 1981, it was rapidly drying up. This reduction in water volume certainly increased larval density and could have induced cannibal morphs as proposed by Collins and Cheek. Similarity in the diet of typical morphs between years makes food an unlikely primary inducer of cannibalism.

Our food habits results are similar to Rose and Armentrout's (1976) in that typical larvae ate large numbers of *Daphnia* in addition to most other available prey and that cannibal morphs ate larger prey. Rose and Armentrout also found that all 30 cannibal morph stomachs they examined had salamander remains and that salamanders ingested were commonly the same size as cannibals. On the contrary, we found salamanders were ingested more in accordance with their availability in the environment and that ingested salamanders were one half the size or less of cannibals.

Much attention has been paid to effects of food and density on growth rates, survivorship to metamorphosis, and size at metamorphosis in typical *Ambystoma* larvae and various species of tadpoles (Wilbur, 1972, 1980; Semlitsch and Caldwell, 1982, and references therein). Our results concur with Rose and Armentrout's (1976) observation that cannibalistic morphs grow faster than typical morphs. High growth rates of individuals with cannibalistic traits may be explained by extrinsic factors of increased prey availability due to having broader heads and larger mouths (*i.e.*, gape-limited predation, *see* Zaret, 1980) and reduction in competitors for other prey due to eating conspecifics (Heusser, 1976; Crump, 1983). Intrinsic genetically induced factors such as hormone levels may also be causative.

Because cannibalistic morphs were relatively rare, we did not observe any undergoing metamorphosis and we do not know whether any succeeded in metamorphosing before Marina Marsh dried. We are fairly certain that no typical larvae were large enough to metamorphose (*see* Wilbur and Collins, 1973). However, Rose and Armentrout (1976) suggest that cannibalistic morphs are slow to metamorphose. If true, advantages due to faster growth rates would be reduced or negated by slower metamorphosis times. On the other hand, if metamorphosis simply depends upon being larger than some threshold body size, cannibalistic morphs should reach that size earlier and have a higher rate of survival under drying marsh conditions.

Both cannibalistic *Ambystoma tigrinum* and *Scaphiopus* sp. morphs are typically associated with drier conditions (*e.g.*, Pierce *et al.*, 1983; Bragg, 1965), but their large



Fig. 2. — Growth of typical *Ambystoma t. tigrinum* larvae collected in 1980(a) and typical and cannibalistic larval morphs collected in 1981(b). Lines here represent growth trends of the population as a whole

size, increased mouth gape, high growth rates and early metamorphosis may also be advantageous under wetter conditions. We then ask why are cannibalistic *A. tigrinum* morphs not present, or at least more common, in the more mesic Midwestern and Eastern portions of the range of the species, and why was the morph not present in our population in 1980? Avoiding group selection arguments (*see* Rose and Armentrout, 1976, for a caution), Pierce *et al.* (1981) use kin selection to argue that if only a few females lay eggs in any pond, cannibals would have a high probability of eating siblings and reducing their own inclusive fitness during nondrought conditions. We propose a second hypothesis not dependent on the assumption of few breeding females. During metamorphosis many amphibians are particularly susceptible to predation and have evolved synchronous metamorphosis as an antipredator strategy (*see* Arnold and Wassersug, 1978, for details). In synchronous metamorphosis animals nearest the mean have a higher probability of surviving and are selected for, while animals at the extremes (*i. e.*, the earliest and latest metamorphosing individuals) are selected against. Clearly, for cannibalistic morphs, early metamorphosis, which is apparently their major advantage under drying conditions, would be a great disadvantage under nondrought conditions. During drought years, however, the critical factor for each salamander is not what happens to it after leaving the pond, but rather just surviving to metamorphosis, which appears to be the adaptive significance of cannibalistic morphs.

TABLE 2.—A comparison of food habits between typical *Ambystoma t. tigrinum* larvae sampled in 1980 and typical and cannibalistic morphs sampled in 1981. Prey items are in approximately increasing order of size based upon length or weight

Prey	1980		1981		1981	
	Typical morphs		Typical morphs		Cannibalistic morphs	
	\bar{x} /stomach	SE	\bar{x} /stomach	SE	\bar{x} /stomach	SE
Ostracoda	117.1	(32.5)	2.9	(0.4)	0.1	(0.1)
<i>Daphnia</i> sp.	250.4	(110.7)	105.3	(22.9)	0.1	(0.1)
Copepoda	1.3	(0.4)	7.4	(1.3)	0.1	(0.1)
<i>Chaoborus</i> larvae	10.4	(1.4)	0.1	(0.0)	0.1	(0.1)
Dipteran adults	trace		trace		—	—
Dipteran larvae/pupae (excluding <i>Chaoborus</i> sp.)	1.7	(0.4)	3.9	(0.6)	2.2	(1.5)
<i>Hyallolela</i> sp.	1.9	(0.4)	0.3	(0.1)	—	—
Coleopteran adults	trace		0.2	(0.1)	—	—
Ephemeropteran naiads	0.7	(0.2)	0.1	(0.0)	—	—
Zygopteran naiads	0.6	(0.1)	trace		—	—
Trichopteran adults	—	—	trace		—	—
Trichopteran larvae	—	—	trace		—	—
Snails (<i>Gyraulis</i> sp., <i>Physa</i> sp.)	0.8	(0.2)	3.5	(0.6)	1.8	(1.6)
Coleopteran larvae	0.2	(0.1)	0.5	(0.1)	—	—
Corixidae	0.6	(0.1)	1.6	(0.4)	0.5	(0.2)
Notonectidae	0.2	(0.1)	0.2	(0.1)	0.5	(0.5)
Oligochaeta	0.1	(0.1)	—	—	—	—
Pelecypoda (<i>Sphaerium</i> sp.)	0.1	(0.0)	trace		—	—
Hirudinea	0.1	(0.0)	—	—	—	—
Anisopteran naiads	0.3	(0.1)	—	—	—	—
Crayfish (<i>Orconectes</i> sp.)	—	—	trace		0.1	(0.1)
<i>Rana pipiens</i> tadpoles	—	—	—	—	0.3	(0.2)
<i>A. t. tigrinum</i> larvae	—	—	—	—	0.7	(0.3)

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