Time to Metamorphosis as a Function of Larval Size in a Population of Ambystoma tigrinum Salamanders Consisting of Cannibal and Typical Morph Phenotypes

Michael J. Lannoo
Ohio University

Michael P. Sweet
Ohio University

Nancy M. Ladehoff
Ohio University

Edmund S. Fangman
Ohio University

Let us know how access to this document benefits you

William B. Collins
Ohio University

Recommended Citation

Time to Metamorphosis as a Function of Larval Size in a Population of *Ambystoma tigrinum* Salamanders Consisting of Cannibal and Typical Morph Phenotypes

MICHAEL J. LANNOO, MICHAEL P. SWEET, NANCY M. LADEHOFF, EDMUND S. FANGMAN, and WILLIAM B. COLLINS

Department of Zoological and Biomedical Sciences, Ohio University, Athens, Ohio 45701

Salamander larvae of the species *Ambystoma tigrinum* are dimorphic in northwestern Iowa. In addition to common typical morphs, there exist rare, specialized cannibal morphs, which are induced environmentally by crowding. Cannibal morph phenotypes are characterized morphologically by their large size, proportionately large heads and hypertrophied vomerine teeth, and behaviorally by facultative cannibalism. During metamorphosis amphibians are particularly sensitive to predation. To help understand why cannibal morphs are uncommon, we have raised cannibal and typical morphs in isolation and under crowded conditions to compare the timing and duration of metamorphosis between these morphs. Results show that larger larvae, most of which exhibit characteristics intermediate between cannibal and typical morphs, and three true cannibal morphs, do not exhibit a discrete time to metamorphosis; they are among the first, but not the first animals to metamorphose. Therefore cannibal morphs may be no more vulnerable to predation than typical morphs during this critical period, and we do not consider that our "metamorphic bottleneck" hypothesis is supported. Overall, crowded larvae metamorphosed an average of three to four days earlier than isolates and were an average of 6 mm smaller at metamorphosis.

INDEX DESCRIPTORS: Amphibian larvae, Cannibal morphs, Ontogeny, Aquatic ecology, Competition, Predation

The time to, and the size at, metamorphosis in amphibians are influenced by environmental conditions. Conspecific density is among the most important of these ecological factors. In general, high densities of conspecifics lengthen the average time to metamorphosis, reduce the average size at metamorphosis, and increase the variation in these characteristics. Intraspecific competition is usually inferred or has been determined to be responsible for this pattern, which has been shown for ambystomatid salamanders (Wilbur, 1976; Wilbur and Collins, 1973; Stenhouse, et al., 1983; Petranka, 1984a, b; Semlitsch and Gibbons, 1985; Stenhouse, 1985; Petranka and Sih, 1986; Semlitsch, 1987a, b), the salamandrid *Notophthalmus* (Morin, et al., 1983; Harris, 1987), and several families of frogs (ranids: Smith-Gill and Bervin, 1979; Collins, 1979; Dash and Hota, 1980; Semlitsch and Caldwell, 1982; Travis, 1984; bufonids: Brockelman, 1969; Breden and Kelley, 1982; hylids: Sokol, 1984; Travis, 1984; pelobatids: Newman, 1989). Recently however, Petranka (1989) has suggested that intraspecific aggression rather than competition for food may explain density dependent effects in *Ambystoma opacum*.

There are exceptions, where high conspecific densities may result in fast growth and early metamorphosis. Within populations of the salamander *Ambystoma tigrinum* (Green), cannibal morph (*sensu* Huxley, 1955; and Collins and Cheek, 1983) phenotypes (Fig. 1) appear to increase their rate of growth, and consequently their size, in response to high densities of conspecifics. For cannibal morphs, which are facultative cannibals, (Powers, 1907; Lannoo and Bachmann, 1984a; but see Rose and Armentrout, 1976), smaller conspecifics are not only competitors but potential prey (Lannoo and Bachmann, 1984a). High densities of salamander larvae occur during times of drought, when lowered water levels concentrate aquatic animals (Lannoo and Bachmann, 1984a).

The question arises: Are cannibal morphs adaptive? [Adaptation here refers to any characteristic of an organism that contributes to its survival and to the survival of its offspring; after Liem and Wake (1985)]. Lannoo and Bachmann (1984a) have argued that aside from a trophic advantage and the reduction of potential competitors through cannibalism (e.g., Fox, 1975; Polis, 1981; Crump, 1983) cannibal morphs should metamorphose earlier than typical morphs, and thus reduce their risk of being caught without a suitable environment as their pond dries. This argument is based on the observation that larger amphibian larvae metamorphose early (Wilbur and Collins, 1973), and that in strongly seasonal environments,

Contribution No. 435 from Iowa Lakeside Laboratory

such as northern Iowa, cannibal morphs are the largest larvae within a population (Lannoo and Bachmann, 1984a). This may not hold for all populations; Rose and Armentrout (1976) report that in Texas, cannibal morphs metamorphose later than typical morphs.

If the cannibal morph phenotype is adaptive, then why aren't all *Ambystoma tigrinum* larvae in these populations cannibalistic? Furthermore, because typical morphs predominate, does this mean that there is a cost to cannibal morphs that can be identified? Lannoo and Bachmann (1984a) have argued that the costs of cannibal morphs may occur at metamorphosis, when the few cannibal morphs in any population would be disadvantaged. In Iowa all of the (presumably typical) larvae within a population can metamorphose simultaneously on one or a few rainy nights in July (similar to the "crash emigrations" described for ranids of the region by Bovbjerg and Bovbjerg, 1964; Bovbjerg, 1965). Most survive because there are many times more salamanders than salamander predators, a theory termed "predator satiation" [see Arnold and Wassersug (1978) for documentation in amphibians]. In this scenario an earlier cannibal morph metamorphosis — distinct from the metamorphosis of typical morph larvae but consisting of only a relatively few animals — would mean a higher risk of predation, and put them at a selective disadvantage compared to the more numerous typical morphs. We term this the "metamorphic bottleneck hypothesis". This hypothesis is critically dependent on the assumption that cannibal morphs metamorphose at a different time (i.e., earlier) than typical morphs. The purpose of the present paper is to test this assumption using laboratory experiments.

MATERIALS AND METHODS

During the summers of 1988 and 1989, *Ambystoma tigrinum tigrinum* larvae were collected by seining the pothole in the basin of the kettle in the Frieda Hafner Preserve (owned by the Nature Conservancy), in northwestern Iowa (43° 23' N, 95° 11' W). The kettlehole, as it is known locally, is located about 8 km SW of The Iowa Lakeside Laboratory, where our experiments were run. Breeding, larval growth, and metamorphosis are seasonal; in this region adult salamanders enter the ponds and marshes to breed in early April, one to two weeks after ice is off. Eggs hatch by late April or early May, then larvae grow and develop for about ten weeks and metamorphose by mid-July (Lannoo and Bachmann, 1984a, b). In deeper marshes in this area some animals overwinter as aquatic larvae
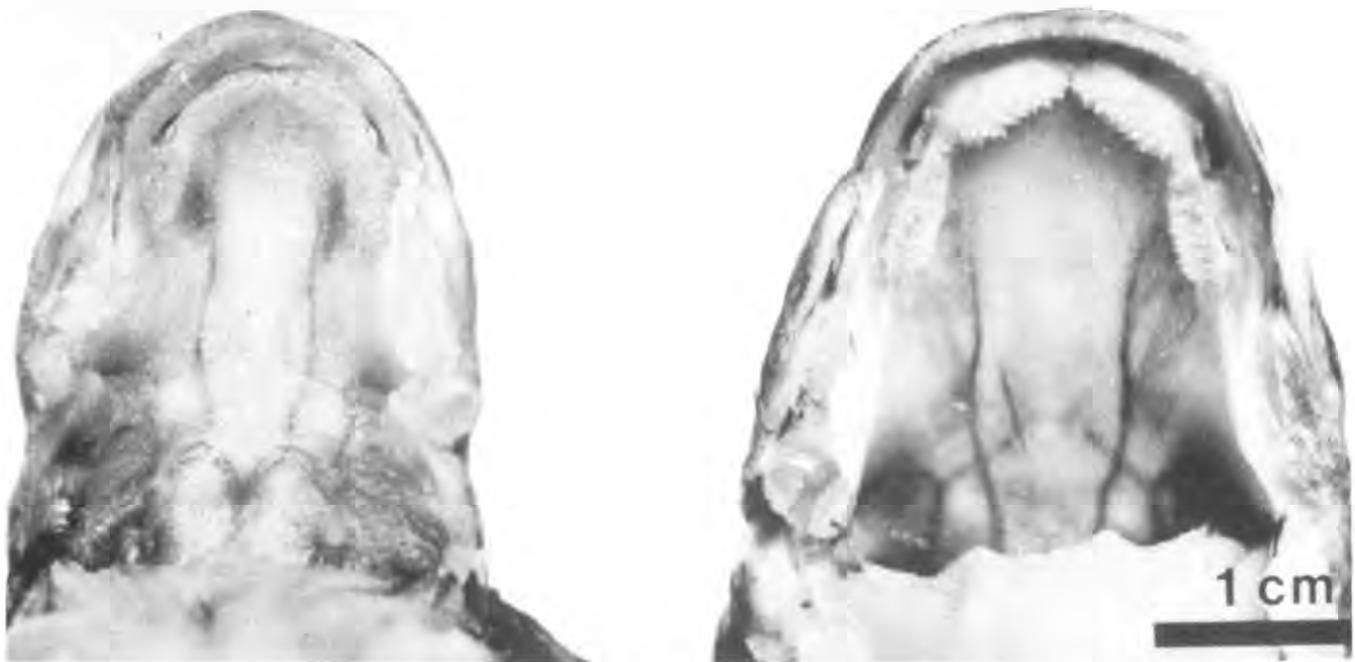
Fig. 1. The differences between typical (left) and cannibal (right) morph *Ambystoma tigrinum* larvae collected in northwestern Iowa. Animals were collected at Gull Point State Park in 1981 nd 1982 and are the same snout vent length (71 mm). Observe that the cannibal morph has a broader head and hypertrophied vomerine teeth. (Reprinted from Lannoo and Bachmann, 1984a, with permission from Notre Dame Press, South Bend, Indiana).

(MJL, unpubl. data). However, our study pond was small and shallow, and in eight years of observation under a variety of water regimes no overwintering larvae have been observed at this site.

In 1988, 219 *Ambystoma tigrinum* larvae were collected on June 20th; in 1989, 260 larvae were collected on June 7th. Within 2h of being collected, the snout vent length (SVL) of each salamander was measured to the nearest millimeter. Many of these larvae were then brought to The Lakeside Laboratory for experimentation.

Experimental Design

Collins (pers. comm.) has recently shown that the classic distinctions between cannibal morphs, with their broad heads and enlarged vomerine teeth, and typical morphs (Powers, 1907) (Fig. 1) in the *A. tigrinum* subspecies *nebulosum* and *mavortium* may not be the result of truly discrete morphologies. According to Collins, who has used principal components analysis on morphometric features, tooth size segregates into two discrete groups while head size and body size vary continuously. These results mean that head size and tooth development vary independently with growth, making the cannibal-typical morph dichotomy the ends of a morphological continuum, with small headed-large toothed, and large headed-small toothed animals intermediate. Because of this, the designation of cannibal or typical morphs based on tooth development, head size, and body size is discretionary (see also Powers, 1907, p. 252).

Rather than rely on our own subjective assessment of the cannibal morph phenotype, and not knowing whether Collins' results apply to our *tigrinum* subspecies (in fact we observe what appears to be a continuum in tooth morphology, and the largest larvae tend towards tooth hypertrophy), to identify cannibal morphs we use, independently, two criteria: 1) larval body size, recognizing first that *A. t. tigrinum* cannibal morphs in northwestern Iowa as described by Lannoo and Bachmann (1984a) are the largest animals in these seasonal populations, and second that the largest animals typically have some degree of vomerine tooth hypertrophy; and 2) the full complement of cannibal morph cranial features including a wide head, fully hypertrophied vomerine teeth, and large size (see Methods

for the rationale behind this approach). This latter group has been unambiguously represented in our observations by only three animals in the two years of our study; even during droughts larvae exhibiting the classic cannibal morphology are rare.

In both years salamanders were put into one of two treatments, either placed individually in cylindrical battery jars, 12.5 cm in diameter, containing about 400 ml of aerated lake water to a depth of 2 cm, or put into groups of four same-sized individuals, in six-liter, all glass rectangular aquaria, 13.5 x 22.2 cm, filled with about 800 ml of aerated lake water to a depth of 2 cm. The density of salamanders in the group treatment was twice that of the individual tanks. The purpose of maintaining low water levels was to induce metamorphosis, an experiment frequently conducted over the years by the Aquatic Ecology class at The Lakeside Laboratory (R.V. Bovbjerg, pers. comm.; see also Semlitsch, 1987a; Semlitsch and Wilbur, 1988).

In 1988, 63 animals ranging in size from 39 - 81 mm SVL were placed in single tanks, 56 animals ranging from 42 - 62 mm SVL were placed into 14 group tanks. In 1989, 50 animals ranging from 28 to 59 mm SVL were placed in single tanks, 68 animals ranging from 32 to 48 mm SVL were placed into 17 group tanks. Group tanks had a narrower size range because four same-sized individuals were not available at the size extremes. Because group tanks consisted of four same-sized individuals, and tanks each represented a different size class, the SVLs for this treatment were not normally distributed at the start of our tests.

Initial SVLs were indicated on the sides of each aquarium, and aquaria were distributed randomly by larval size on a large countertop in a stone laboratory, adjacent to open, screened windows facing north. Temperatures were allowed to fluctuate naturally and ranged from 12 - 30°C. We could measure no temperature gradients across our tanks. These temperatures, on average, were comparable to temperatures in the field, although the daily extremes were not met. In northwestern Iowa, 1988 was a hotter, drier year than 1989. However, with ground water stores already depleted from the 1988

drought, ponds dried earlier in 1989. The first salamanders in the lab metamorphosed at the same time as salamanders in the field, but our impression was that metamorphosis was prolonged in the lab.

Larvae were hand fed on pieces of earthworm and beef liver until they would ingest no more. This food was supplemented once a week with natural invertebrate prey (zooplankton and aquatic insect larvae).

Salamanders were examined twice a day for signs of metamorphosis. Our criterion for metamorphosis was the time when all secondary gill filaments were resorbed. At this stage the gill stalks were usually less than 3 mm long, although larger animals had slightly longer gills. This morphology was associated with crawling out of the water, onto small rocks that were placed in each tank, and with skin shedding. At metamorphosis the SVLs of animals were again measured. To prevent measuring bias, the measurer had no knowledge of the initial size of the animal. Data were recorded by day (the day of collection being day 1) and by treatment [single (1X) or group (4X) tanks]. Metamorphosed animals were returned to the shoreline of the Frieda Hafner Preserve with two exceptions: in 1988, a few larvae were kept and preserved for morphological analysis; in 1989, the kettlehole dried and animals were instead returned to a pond about ¾ mi east of the Preserve. Because the kettlehole dried early, we believe the salamanders that we collected, observed, and returned, represented the entire reproductive success of this population in 1989.

Statistics

The individuals in our population were approximately normally distributed (with the exception of initial SVLs in the 4X treatment) with equal variances and therefore we used parametric statistics — the analysis of variance and t-tests for unpaired samples — to test for significant differences. A priori we established our significance level as $p < 0.05$.

RESULTS

Size Distributions

During both years the distribution of SVLs within populations of *Ambystoma tigrinum* larvae containing individuals with cannibal morph features was approximately normally distributed, with a slight skew — the largest animals were larger than expected based on a normal curve (Fig. 2). This size distribution has been seen in other marshes throughout the region in other years (Lannoo, unpubl. data). These largest individuals typically exhibit, to varying degrees, the broad heads and vomerine tooth development characteristic of cannibal morphs (Lannoo and Bachmann, 1984a). Larvae were collected at smaller sizes in 1989, in part because they were captured two weeks earlier in the year, but also because this region experienced a late spring in 1989, and larvae were younger and less developed.

The Relationship of Initial Size and Growth to Time to Metamorphosis

In 1988, salamanders began metamorphosing on June 27th (seven

Table 1. The relationship between initial larval size (in mm, SVL, with standard error) and metamorphosis. In both years metamorphosed larvae were larger at the time of collection than non-metamorphosed larvae.

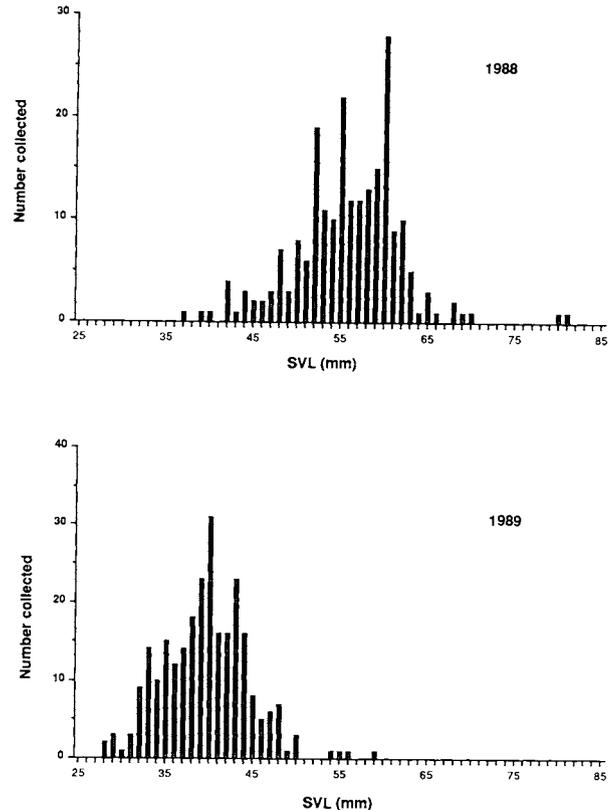|	Metamorphosed	Non-metamorphosed	t	P
1988				
	57.6 (5.6)	48.9 (5.2)	6.2	$<10^{-6}$
	n = 97	n = 19		
1989				
	43.4 (5.3)	38.0 (5.4)	4.9	$<10^{-6}$
	n = 54	n = 58		

Fig. 2. The size distributions of *Ambystoma tigrinum* larvae collected at the Frieda Hafner Preserve kettlehole in 1988 and 1989. Note that in both years larval sizes are approximately normally distributed, with a slight skew towards larger sizes.

days after they were collected), and in 1989, on July 4th (28 days after they were collected). In 1988, our experiments were terminated on August 5th (46 days after collection) and in 1989, on July 28th (53 days after collection). In 1988, 97 salamanders metamorphosed (82%), 19 had not, three died. In 1989, 54 salamanders metamorphosed (51%), 48 had not, 12 died. Mortality in the 4X tanks was usually due to stress or injury brought on by cannibalistic attempts.

Initial Size

In both years larger larvae were the first to metamorphose. These differences were significantly different for both years (Table 1). Most of these large larvae (six of eight larger than 45 mm SVL on July 6th, 1989) exhibited at least partial vomerine tooth hypertrophy and a broadening of their heads. Among the metamorphosing salamanders in 1988, initial size was negatively correlated with time to metamorphosis (Fig. 3; $p < 10^{-6}$). This trend was not apparent in 1989, probably because a lower percentage of animals metamorphosed.

Growth Rates and Size at Metamorphosis

Growth rates were not significantly different between metamorphosed and non-metamorphosed animals in either year (Table 2a). Likewise, SVLs of metamorphosed and non-metamorphosed larvae on the final day of our observations were not significantly different in either year (Table 2b). Growth rates were higher in 1989, but interestingly, mean size at metamorphosis was smaller in 1989.

The Comparison Between 1X and 4X Treatments

The percentage of larvae metamorphosing between treatments was

Table 2. A. The relationship between growth rates (mm/day, SVL, with standard error) of metamorphosed and non-metamorphosed larvae. B. A comparison of the size of animals (mm, SVL, with standard error) at metamorphosis to the size of non-metamorphosing animals at the end of our experiment each year.

A.

	Metamorphosed	Non-metamorphosed	t	P
1988				
	0.38 (0.17)	0.34 (0.08)	1.0	0.30
	n = 97	n = 19		
1989				
	0.43 (0.09)	0.46 (0.10)	1.8	0.08
	n = 54	n = 58		

B.

	Metamorphosed	Non-metamorphosed	t	P
1988				
	63.8 (5.1)	64.7 (4.6)	0.5	0.60
	n = 97	n = 19		
1989				
	59.7 (4.9)	61.3 (5.9)	1.4	0.15
	n = 54	n = 58		

similar within years. In 1988, 83% of the larvae in the 4X treatment metamorphosed, while 84% of the larvae in the 1X treatment metamorphosed. In 1989, 54% of the larvae in the 4X treatment metamorphosed, while 51% of the larvae in the 1X treatment metamorphosed. (These percentages do not include animals that died during the experiments.)

Larvae in the 4X treatment metamorphosed significantly earlier than those in the 1X treatments during both years; the mean difference was between three and four days in both years (Table 3a). These differences were not correlated with growth rates (Table 3b). In 1988, larvae in the 1X treatment grew faster than in the 4X treatment but these differences were not significant. In 1989, larvae in the 4X treatment grew significantly faster than those in the 1X treatment. Taken together these data do not support a correlation between growth rate and time to metamorphosis.

The difference in time (days) to metamorphosis between the 4X and 1X treatments was correlated with size at metamorphosis in both years. Larvae in the 1X treatments were slower to metamorphose (by about three days) but significantly larger (6 mm average) at metamorphosis than those in the 4X treatments (Table 3c).

DISCUSSION

Our experiments were conducted over two field seasons and produced consistent trends. In both years, larger larvae and crowded larvae took less time to metamorphose. Because larger larvae tend to have cannibal morph features, this result initially supported the metamorphic bottleneck hypothesis. However, we found that the three identified full cannibal morphs [using the criteria in Lannoo and Bachmann (1984a)] were among the first, but not the first, to metamorphose. Therefore, at this time we cannot consider that cannibal morphs exhibit a discrete metamorphosis, and conclude that the data do not support the metamorphic bottleneck hypothesis.

Initial Size Distribution

The size (SVL) distribution of *Ambystoma tigrinum* larvae in populations containing cannibal morph characteristics show an approximately normal distribution with a slight skew towards larger sizes — the largest larvae are bigger than expected from a normal distribution (Fig. 2). This curve was also characteristic of a separate population of salamanders located in the Gull Point State Park containing cannibal

morphs in 1982 (Lannoo and Bachmann, 1984a) and 1988 (Lannoo, unpubl. data). Most of these larger larvae, to varying degrees, have the broad heads and vomerine tooth development characteristic of cannibal morphs (Fig. 1).

Time to Metamorphosis

Size. Larger larvae metamorphosed significantly earlier than smaller ones in both years (Table 1; Fig. 3). This is in agreement with the observations of most authors working with both anurans and urodeles, and has led to the concept of a critical size threshold or optimum size for metamorphosis (Wilbur and Collins, 1973; Collins, 1979; Werner, 1986).

Cannibal morphs may vary their relative time to metamorphosis compared to typical morphs across their range. In our population cannibal morphs were among the first to metamorphose. Yet, according to Rose and Armentrout (1976), cannibal morphs in Texas appear to metamorphose later than small morphs. Powers (1907) also mentions that in Nebraska cannibal morphs are slow to metamorphose.

Growth Rate. Growth rates (mm/day, SVL) were not significantly different between animals that metamorphosed and those that did not (Table 2). Therefore we assume that growth rate differences did not affect the time to metamorphosis.

Size at Metamorphosis

At first it may seem contradictory that there were not significant differences between the size of larvae at metamorphosis and the final size of non-metamorphic larvae if, as we report, initially larger larvae metamorphosed first and growth rates were the same. However, larvae that metamorphosed reached this size sooner than non-metamorphosed larvae. We assume that most of the larvae that had not metamorphosed at the end of our observations would have done so had we continued our observations, although larvae in this region are known to overwinter (Lannoo, unpublished data).

Table 3. A comparison of the 1X and 4X treatments: A. Time to metamorphosis (in days); B. Growth rates (mm/day SVL); C. Size at metamorphosis (mm SVL). All means include standard errors.

A. Days to Metamorphosis

	1X	4X	t	P
1988				
	18.4 (8.0)	15.1 (8.1)	2.1	0.04
	n = 53	n = 44		
1989				
	39.7 (6.0)	36.1 (5.4)	2.4	0.02
	n = 53	n = 44		

B. Growth Rate

	1X	4X	t	P
1988				
	0.41 (0.16)	0.35 (0.17)	1.8	0.08
	n = 53	n = 44		
1989				
	0.39 (0.08)	0.46 (0.09)	2.8	±0.01
	n = 53	n = 44		

C. Size at Metamorphosis

	1X	4X	t	P
1988				
	66.4 (5.0)	60.7 (3.3)	6.5	$<10^{-6}$
	n = 53	n = 44		
1989				
	63.0 (4.1)	57.1 (3.9)	5.4	$<10^{-5}$
	n = 53	n = 44		

Crowding

Early Metamorphosis. Crowded larvae (4X treatment) metamorphosed significantly earlier than larvae kept individually (1X treatment) in both years (Table 3a). These differences averaged three to four days. Growth rates do not appear to be responsible for this trend: in 1988, 1X and 4X animals grew at the same rate, while in 1989, 4X animals grew significantly faster (Table 3b). Perhaps then, time to metamorphosis is partially dependent on social factors such as crowding. Breden and Kelley (1982) have shown that in *Bufo*, an increase in the interactions among pre-metamorphic tadpoles lengthens the duration of metamorphosis. In *Ambystoma* this effect may be reversed.

Size. In addition to decreasing the time to metamorphosis, crowding decreases the size at metamorphosis (Table 3c.). Again the magnitude of these differences was similar between years, with salamanders in the 1X treatments metamorphosing about 6 mm SVL larger. We make these statements tentatively: these differences may be partially related to the initial differences in size at the beginning of our observations; in 1988 larvae in the 1X tanks averaged 2.4 mm larger than animals in the 4X tanks (57.2 to 54.8 mm SVL), in 1989 1X animals were 3.1 mm larger (58.9 to 55.9 mm SVL).

The size at metamorphosis varies among years: 1989 larvae were smaller than 1988 larvae (Table 3c). Taken together, these data on time to, and size at, metamorphosis support the idea that metamorphosis in populations containing cannibal morphs is influenced to some extent by environmental factors.

A Critique of the Experimental Design: A Role for Crowding in Maintaining Cannibal Morphs?

In our experiments we purposely isolated or semi-isolated our animals and controlled their food and temperature regimes. However, by doing this we reduced or canalized social interactions. At this point we do not know whether the cannibal morphology represents an irreversible shift in the developmental program of these animals, or whether cannibal morph features can revert to typical morph features once the environmental factors that induce the cannibal morph are removed (as suggested by Powers, 1907: p. 265). If the latter case is true, further experiments controlling for this contingency need to be done.

In the 4X tanks, there were several cannibalistic attempts that were unsuccessful because of the similar size between predator and prey salamanders. Isolates, of course, had no interactions with conspecifics. And although, as much as possible, we attempted to mimic natural conditions, we realize now that because larvae were isolated or semi-isolated, they may not have responded under our laboratory conditions in the same manner that they would have under more social field conditions.

A Note on the Distribution of Cannibal Morphs and a Plea for Conservation

Cannibal morphs have been described in *Ambystoma tigrinum* in the United States for the southwestern subspecies *A. t. mavortium* and *A. t. nebulosum*, and western populations of *A. t. tigrinum*. Animals from eastern and northern populations of *A. t. tigrinum* kept under crowded conditions (i.e., regimes that produce cannibal morphs in western populations) did not exhibit cannibal morph characteristics (Lannoo, et al., 1989). Presumably, the genes for cannibal morphs are the same among these three subspecies but are either not present or not expressed in eastern populations of *A. t. tigrinum*. Our reports have been the only documented evidence of cannibal morph *Ambystoma tigrinum* larvae in Iowa, and in *A. t. tigrinum* across its range, which includes much of the eastern United States. In fact, Iowa may mark the eastern boundary of this phenotype; collections made at the Ledges State Park, west of Ames in 1979 and 1980 — when cannibal morphs were first collected in northwestern Iowa — did not contain cannibal morphs (MJL, unpubl. data).

Clearly, more work needs to be done before we will fully understand the biology of cannibal morphs. We know of only two *Ambystoma tigrinum* populations containing cannibal morphs in Iowa, yet our attempts to gain legal protection for these animals have not been successful. The laws governing endangered and protected species in Iowa do not recognize polymorphisms. In northwestern Iowa, natural amphibian populations have declined, largely because their habitats are being used to raise game fish (Bovbjerg, 1965), but also, as in the case of *Rana pipiens*, through potential competition from recent introductions of non-native species (i.e., the bullfrog *Rana catesbeiana*). We hope that through education it will be recognized that the native amphibian populations fulfill ecological roles, and that the ecologies and evolutionary histories of some types, including the rare cannibal morph *A. tigrinum* larvae, are incompletely understood. These animals should be allowed to persist.
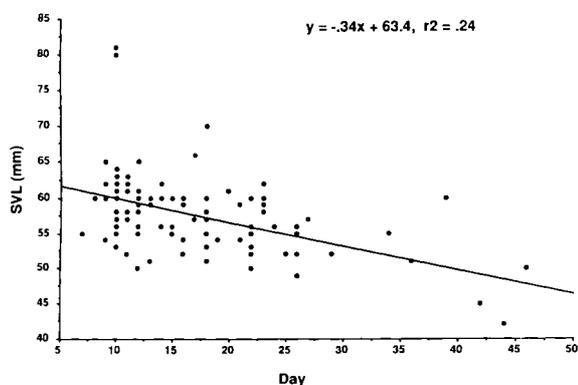
Fig. 3. The relationship between size at capture and time to metamorphosis in 1988. Observe that larger larvae metamorphosed sooner. (The probability of the slope = 0 is <10⁻⁶.)

$y = -.34x + 63.4, r2 = .24$

REFERENCES

ARNOLD, S.J. and R.J. WASSERSUG. 1978. Differential predation on metamorphic anurans by garter snakes (*Thamnophis*): social behavior as a possible defense. Ecology 59;1014-1022.

BREDEN, F. and C.H. KELLY. 1982. The effect of conspecific interactions on metamorphosis in *Bufo americanus*. Ecology 63:1682-1689.

BOVBJERG, R.V. 1965. Experimental studies on the dispersal of the frog, *Rana pipiens*. Proc. Iowa Acad. Sci. 72:412-418.

BOVBJERG, R.V. and A.M. BOVBJERG. 1964. Summer emigrations of the frog *Rana pipiens* in Northwestern Iowa. Proc. Iowa Acad. Sci.: 71:511-518.

BROCKELMAN, W.Y. 1969. An analysis of density effects and predation in *Bufo americanus* tadpoles. Ecology 50:632-644.

COLLINS, J.P. 1979. Intrapopulation variation in the body size at metamorphosis and timing of metamorphosis in the bullfrog, *Rana catesbeiana*. Ecology 60:738-749.

COLLINS, J.P. and J.E. CHEEK. 1983. Effect of food and density on development of typical and cannibalistic salamander larvae in *Ambystoma tigrinum nebulosum*. Am. Zool. 23:77-84.

CRUMP, M. 1983. Opportunistic cannibalism by amphibian larvae in temporary aquatic environments. Am. Nat. 121:281-289.

DASH, M.C. and A.K. HOTA. 1980. Density effects on survival, growth rate, and metamorphosis of *Rana tigrina* tadpoles. Ecology 60:1025-1028.

FOX, L.R. 1975. Cannibalism in natural populations. Annu. Rev. Ecol. Syst. 6:87-106.

HARRIS, R.N. 1987. Density-dependent paedomorphosis in the salamander *Notophthalmus viridescens dorsalis*. Ecology 68:705-712.

HUXLEY, J.S. 1955. Morphism and Evolution. Heredity 9:1-52.

LANNOO, M.J. and M.D. BACHMANN. 1984a. Aspects of cannibalistic morphs in a population of *Ambystoma tigrinum* larvae. Am. Midl. Nat. 112:103-109.

LANNOO, M.J. and M.D. BACHMANN. 1984b. On flotation and air breathing in *Ambystoma tigrinum* larvae: stimuli for and the relationship between these behaviors. Can J. Zool. 62:15-18.

LANNOO, M.J., L. LOWCOCK and J.P. BOGART. 1989. Sibling cannibalism in noncannibal morph *Ambystoma tigrinum* larvae and its correlation with high growth rates and early metamorphosis. Can J. Zool. 67:1911-1914.

LIEM, K.F. and D.B. WAKE. 1985. Morphology: Current approaches and concepts. Chptr. 18. In: Functional Vertebrate Morphology. (M. Hildebrand, D.M. Bramble, K.F. Liem, and D.B. Wake, eds). Belknap, Harvard, Cambridge, pp. 366-377.

MORIN, P.J., H.M. WILBUR and R.N. HARRIS. 1983. Salamander predation and the structure of experimental communities: responses of *Notophthalmus* and *Microcrustacea*. Ecology 64:1430-1436.

NEWMAN, R.A. 1989. Developmental plasticity of *Scaphiopus couchii* tadpoles in an unpredictable environment. Ecology 70:1775-1787.

PETRANKA, J.W. 1984a. Sources of interpopulational variation in growth responses of larval salamanders. Ecology 65:1857-1865.

PETRANKA, J.W. 1984b. Incubation, larval growth, and embryonic and larval survivorship of smallmouth salamanders *(Ambystoma texanum)* in streams. Copeia 1984:862-867.

PETRANKA, J.W. 1989. Density-dependent growth and survival of larval *Ambystoma:* evidence from whole-pond manipulations. Ecology 70:1752-1767.

PETRANKA, J.W. and A. SIH. 1986. Environmental instability, competition, and density-dependent growth and survivorship of stream dwelling salamander. Ecology 67:1289-1296.

PIERCE, B.A., J.B. MITTON, and F.L. ROSE. 1983. Head shape and size in cannibal and noncannibal larvae of the tiger salamander from west Texas. Copeia 1983:1006-1012.

POLIS, G.A. 1981. The evolution and dynamics of intraspecific predation, Annu. Rev. Ecol. Syst. 12:225-251.

POWERS, J.H. 1907. Morphological variation and its causes in *Ambystoma tigrinum*. Stud. Univ. Nebr. 7:197-274.

ROSE, F.L. and D. ARMENTROUT. 1976. Adaptive strategies of *Ambystoma tigrinum* Green inhabiting the Llano Estacado of West Texas. J. Anim. Ecol. 45:713-729.

SEMLITSCH, R.D. 1987a. Paedomorphosis in *Ambystoma talpoideum:* effects of density, food, and pond drying. Ecology 68:994-1002.

SEMLITSCH, R.D. 1987b. Density-dependent growth and fecundity in the paedomorphic salamander *Ambystoma talpoideum*. Ecology 68:1003-1008.

SEMLITSCH, R.D. and J.P. CALDWELL. 1982. Effects of density on growth, metamorphosis, and survivorship in tadpoles of *Scaphiopus holbrooki*. Ecology 63:905-911.

SEMLITSCH, R.D. and J.W. GIBBONS. 1985. Phenotypic variation in metamorphosis and paedomorphosis in the salamander *Ambystoma talpoideum*. Ecology 66:1123-1130.

SEMLITSCH, R.D. and H.M. WILBUR. 1988. Effects of pond drying time on metamorphosis and survival in the salamander *Ambystoma talpoideum*. Copeia 1988:978-983.

SMITH-GILL, S.J. and K.A. BERVEN. 1979. Predicting amphibian metamorphosis. Am. Nat. 113:563-585.

SOKOL, A. 1984. Plasticity in the fine timing of metamorphosis in tadpoles of the hylid frog, *Litoria ewingi*. Copeia 1984:868-872.

STENHOUSE, S.L. 1985. Interdemic variation in predation on salamander larvae. Ecology 66:1706-1717.

STENHOUSE, S.L., N.G. HAIRSTON and A.E. COBEY. 1983. Predation and competition in *Ambystoma* larvae: field and laboratory experiments. J. Herpetol. 17:210-220.

TRAVIS, J. 1984. Anuran size at metamorphosis: experimental test of a model based on intraspecific competition. Ecology 65:1155-1160.

WERNER, E.E. 1986. Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. Am. Nat. 128:319-341.

WILBUR, H.M. 1976. Density-dependent aspects of metamorphosis in *Ambystoma* and *Rana sylvatica*. Ecology 57:1289-1296.

WILBUR, H.M. and J.P. COLLINS. 1973. Ecological aspects of amphibian metamorphosis. Science 1982:1305-1314.