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“Paedocannibal” Morph Barred Tiger Salamanders (*Ambystoma tigrinum mavortium*) from Eastern South Dakota

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ABSTRACT.—We report characteristics of a previously unknown population of *Ambystoma tigrinum mavortium* (barred tiger salamander) from eastern South Dakota, a location that extends the formerly known range of this subspecies about 150 km north. This population contains paedotypic animals and a small percentage of cannibal morphs. At least one cannibal morph was paedotypic. The vomerine tooth hypertrophy characteristic of cannibal morphs described here differs from the cannibal morph *A. t. tigrinum* from nearby (about 160 km) northwestern Iowa; in particular the pair of caudolateral tooth ridges has smaller teeth in individuals from the *A. t. mavortium* population. The study wetland is located near the convergence of four recognized (pending revision) tiger salamander subspecies (*A. t. diaboli* and *A. t. melanosticum* in addition to *A. t. mavortium* and *A. t. tigrinum*), making it an excellent region to examine subspecific morphological features in light of shared ecological factors. We suggest creating a formal nomenclatural distinction between cannibal morph larval phenotypes and cannibal morph paedotypic phenotypes.

INTRODUCTION

Salamanders are remarkable for their phenotypic plasticity (e.g., Powers, 1907; Dunn, 1940; Rose and Armentrout, 1976; Collins *et al.*, 1993). The most variable of all salamanders is probably the tiger salamander (Ambystomatidae: *Ambystoma tigrinum*). The now classic descriptions by Powers (1907) of tiger salamander phenotypes encompass branchiate cannibal and typical morphs, including both larvae and paedotypic animals (terminology of intraspecific heterochrony following Reilly *et al.*, 1997 after Alberch *et al.*, 1979), in addition to adult metamorphic animals.

The cannibal morph phenotype occurs naturally from southwestern United States' populations of Arizona tiger salamanders (*A. t. nebulosum*), barred tiger salamanders (*A. t. mavortium*), and from a single metapopulation of eastern tiger salamanders (*A. t. tigrinum*) in northwestern Iowa (Powers, 1907; Rose and Armentrout, 1976; Collins and Cheek, 1983; Lannoo and Bachmann, 1984; Reilly *et al.*, 1992). Cannibal morphs in Stebbin's tiger salamanders (*A. t. stebbensi*) and an additional population of *A. t. tigrinum* from Indiana have been induced in the laboratory (J. P. Collins and D. Pfennig, respectively, pers. comm.). Here, we report a population of tiger salamanders, defined as *A. t. mavortium* by their adult color patterns, gill raker counts and mitochondrial DNA, from east central South Dakota that contains individuals that exhibit both cannibal morph and paedotypic features. This population was previously unknown and represents the northernmost reported population of cannibal morphs in any tiger salamander subspecies.

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We describe characteristics of this *A. t. mavortium* population including: (1) features of its wetland habitat; (2) a comparison of the size and seasonal occurrence of putative paedotypic and larval animals; (3) the frequency of cannibal morphs; (4) a category of animals that exhibits a trophic morphology intermediate between cannibal and typical morphs; (5) variation in color patterns; (6) a skeletochronological analysis of age of paedotypics; (7) histological and gross anatomical analyses of gonads to determine sexual maturity; and (8) mitochondrial DNA analysis. We compare these features of this *A. t. mavortium* population with a population of *A. t. tigrinum* from northwestern Iowa that contains cannibal morphs, and a population of *A. t. diaboli* from east central North Dakota that contains paedotypic animals. We discuss which features can be ascribed reasonably to subspecies tendencies and which features may be due to ecological constraints imposed by the Prairie Pothole Region. Finally, we suggest making a formal nomenclatural distinction between cannibal morph larval phenotypes and cannibal morph paedotypic phenotypes.

METHODS

This project was initially part of a larger study designed to evaluate the effectiveness of restored, created and natural wetlands in promoting biodiversity (Larson, 1997). In this study, amphibian populations were 1 of 7 floral and faunal assemblages chosen to evaluate each of the wetland types. When the unusual features (*see below*) of the branchiate tiger salamander population were realized in August of 1996, more attention and additional sampling effort were given to these animals.

Habitat features.—Salamanders were collected from the Kneip Waterfowl Production Area (WPA) in Brookings County, 1 mile north of Arlington, South Dakota. Brookings County is located in the Prairie Coteau physiographic region of the Prairie Pothole Region and is characterized by a rolling postglacial landscape where small isolated wetlands are common. Tiger salamanders use these wetlands for breeding and are abundant.

Wetland characterization.—The Kneip WPA has a total land area of about 30 ha including a 13-ha restored wetland. Restoration began in October 1990 by closing a 70- to 90-y-old tile drainage system. Water depth is now approximately 1.5 m throughout much of the wetland with a maximum of 3 m in one area. For details of the vegetation of this wetland and the composition of its invertebrate fauna *see* Larson (1997). In addition to tiger salamanders, fathead minnows (*Pimephales promelas*) were present in 1995 and 1996.

Collection of salamanders.—Salamanders were collected by using a combination of aquatic funnel trapping and seining. The effectiveness of unbaited funnel traps in capturing amphibian larvae has been documented (Shaffer *et al.*, 1994). Traps were set with a portion of the trap above the surface of the water to allow the animals to breathe atmospheric oxygen.

In 1995, a single trap was set in the wetland on two occasions: 19–22 May and 30–31 May. In 1996, a single trap was placed in the wetland on four separate occasions: 5–6 May, 5–6 August, 31 August–3 September and 3–6 September. Some salamanders captured were cannibal morphs (*see below*). To capture additional cannibal morphs, six traps were set on 6–7 September 1996. On 7 Sept. the traps were emptied, the wetland was seined and fifty-six animals were taken back to the laboratory, where mass (g), total body length (mm TL), snout to vent length (mm SVL) and snout to gill opening length (mm SG) of each animal were measured. A preliminary characterization of morphotype (paedotypic and/or cannibal morph) was made based on body size, head shape and size, cloacal development and tooth morphology. Thirty-two representative branchiate animals were maintained in South Dakota and transported live to Indiana for additional examination.

Pitfall traps used in combination with drift fences (Campbell and Christman, 1982) were

set on land to determine the timing of metamorphosis in this population. To trap newly metamorphosed animals, an 8-m drift fence was placed parallel to and approximately 3 m from the shoreline and a second 8-m fence was positioned perpendicular to the first to form an "L". A pitfall trap (10 L) was placed at the distal end of each leg, and in the corner of the intersection. This array was set on 18 and 19 May in 1995, and 29 April, 15, 21, and 24 May and 5 and 29 August in 1996.

Subspecies diagnosis.—The published ranges of *A. t. tigrinum*, *A. t. melanostictum* and *A. t. diaboli* (subspecies designations pending revision, E. Routman, pers. comm.) converge near Brookings County (Conant and Collins, 1991). The closest *A. t. mavortium* population to Brookings is from northeastern Nebraska. However, the status of subspecies in the *A. tigrinum* complex has not been well characterized in South Dakota due to the scarcity of specimens from critical regions and the difficulty in identifying subspecies (Dunlap, 1967). While Dunlap (1967) described a highly variable population from the Brookings County area, which he suggested could be attributed to interbreeding among the three subspecies, it is possible that Dunlap's (1967) population is *A. t. mavortium*, as described here (*see below*).

Based on the color pattern of metamorphosed animals and gill raker counts in branchiate animals (Dunn, 1940; Stebbins, 1985; Conant and Collins, 1991), we tentatively identified this population as *A. t. mavortium* (barred tiger salamanders, this initial identification was confirmed, *see below*); however, we had reservations. Some gill raker counts (16–20) were in the range of *A. t. tigrinum* (Collins *et al.*, 1980), and this population is located out of the published distributional range of *A. t. mavortium* (Stebbins, 1985; Conant and Collins, 1991). Furthermore, this region represents the convergence of several tiger salamander subspecies (*see above*), and Dunn (1940) reports that transitions occur between subspecies in this region. To confirm our initial diagnosis, we anesthetized a subset of animals collected from 7 September 1996 and from each animal removed an external gill and preserved it in 70% ethanol. These tissues were then shipped to San Francisco State University for mitochondrial DNA analyses.

Total cellular DNA was extracted from preserved tissue using a salt extraction protocol. A 400 bp double stranded fragment was amplified using polymerase chain reaction (PCR) from an insert between the threonine and proline tRNA genes of the mitochondrial DNA (mtDNA). Primers were designed based on primer sequence from Shaffer and McKnight (1996) [THR 5' AAACATCGATCTTGTAAGTC 3'; PRO 5' AGAATTTTGGCTTTGGTGCC 3', with a 40 bp G–C clamp attached to the 5' end of PRO (Norman *et al.*, 1994)]. The amplified product was screened using Denaturant Gradient Gel Electrophoresis (DGGE) to determine variable haplotypes. These results were compared to results previously obtained from populations of *A. t. tigrinum* from Dickinson County, Iowa, of *A. t. diaboli* from eastcentral North Dakota, of *A. t. melanostictum* from Cherry County, Nebraska, and from St. Louis Co., Missouri, and of *A. t. mavortium* from Frontier Co., Nebraska, and Valley Co., Missouri.

Morphotype diagnosis.—Preliminary diagnoses of paedotypic animals were made on 56 animals collected on 7 September 1996, using gross morphological characteristics, including overall size and cloacal morphology. However, cloacal size does not vary obviously in females (but *see Trauth et al.*, 1994 for a histological analysis) and appeared to decrease substantially in males between the August and September sampling dates, making it difficult to confirm sexual maturation in our September samples based solely on this criterion.

Thirty-two branchiate animals collected on 7 September 1996 were sent to Indiana for morphological and histological analyses. These animals included suspected cannibal morphs and suspected paedotypes. Two animals metamorphosed before reaching Indiana.

Seven branchiate animals were anesthetized in a solution of 3-aminobenzoic ethyl acid ester (Sigma Chemical Company, St. Louis) diluted 1:10,000 in aged tap water and euthanized by transcathal perfusion of 0.1M phosphate buffered saline (PBS) followed by 4% paraformaldehyde dissolved in PBS. Seventeen of the remaining branchiate animals were anesthetized and preserved in 10% formaldehyde. The remaining 6 branchiate and 2 metamorphosed animals were maintained overwinter. Preserved animals were then dissected. In the 24 dissected branchiate animals, gonadal size was examined grossly and the maximum width of gonads at the midpoint of their length was measured. Gonadal development was examined in four males (80, 100, 110, 125 mm SVLs) and one female (135 mm SVL) using standard histological techniques (dehydration, paraffin embedding, sectioning, rehydration, staining, dehydration and coverslipping using Permount® [Fisher Chemical, Fair Lawn, New Jersey] as the mounting medium; Kiernan, 1990). Ovaries were stained with 0.1% cresyl violet while testes were stained with Harleco® hematoxylin and eosin (EM Diagnostic Systems, Gibbstown, New York 08027). Sectioning was done at 12 µm on a Lipshaw model 45 rotary microtome. Sections were mounted, examined, and representative portions were photographed using a Zeiss Jenalumar photomicroscope and Kodak Tmax 100 film.

Cannibal morph phenotypes were determined by a qualitative assessment of head shape, head width and vomerine tooth morphology. In an effort to quantitatively assign morphotype, head width 5-mm rostral to the eye, head width 5-mm caudal to the eye and SVL were considered. The usual interpretation of a dimorphism between cannibal and typical morphs (sensu Rose and Armentrout, 1976; Collins and Cheek, 1983; Lannoo and Bachmann, 1984) has been modified to include a category of intermediate phenotypes (e.g., Lannoo *et al.*, 1990), which includes animals with moderately hypertrophied vomerine teeth and moderately enlarged head widths. Indeed, Powers (1907) recognized such intermediate animals.

Because this *A. t. mavortium* population contains cannibal morphs, and because the origin of cannibal morph *A. t. tigrinum* remains an open question, we considered the proximity (160 kilometers) of Brookings County to the Iowa Lakeside Laboratory, where the only naturally occurring population of cannibal morph *A. t. tigrinum* has been identified (Lannoo and Bachmann, 1984; Lannoo *et al.*, 1990; Lannoo, 1996). Tooth morphology of animals from this South Dakota population of *A. t. mavortium* was compared to that of *A. t. tigrinum* from Iowa Lakeside Laboratory.

Color patterning.—Ground color and patterns of pigmentation were noted for each class of animals (paedotypic or larval, cannibal or typical) in an attempt to determine if morphotype can be characterized by color pattern (see Rose and Armentrout, 1976).

Food habits.—Six suspected cannibal morphs collected in August, 1996, were dissected to determine stomach contents. A further assessment of food habits was made using gastric lavage on live animals captured in September, 1996.

Skeletochronology.—Skeletochronology can be used in animals that exhibit annual cycles of growth, typically associated with warmer or wetter periods, and torpor or estivation associated with cooler or drier periods. In making age estimations from bone annuli, it is generally assumed that annuli are permanent. However, bone tissue may be resorbed from the marrow cavity (endosteal resorption core), erasing evidence of younger ages. Because of this, interpretations of age from skeletochronological evidence must be made cautiously (e.g., Halliday and Verrell, 1988; Wake and Castanet, 1995; Castanet *et al.*, 1996).

Skeletochronological analyses were done on forelimbs removed from 3 perfusion-fixed animals: 2 cannibal morphs—1 large female (SVL = 130 mm) and 1 smaller male (SVL = 95 mm)—and 1 large male animal with an intermediate phenotype between typical and cannibal morphs (SVL = 125 mm) were examined. Each humerus was bisected, immersed in Decalcifier II® (Surgipath Medical Industries, Inc., Richmond, IL) for 25 minutes (Cas-

tanet *et al.*, 1996), mounted, dehydrated, embedded in paraffin and sectioned through the diaphysis. About 10 sections at 20 μm thickness were taken from each bone. The best sections (clearly demarcated lag lines) were then stained in hematoxylin and eosin, dehydrated, mounted, examined and photographed as described above, except that differential interference contrast microscopy was used to highlight bone features.

RESULTS

Collecting animals.—Aquatic funnel trapping in 1995, on 30–31 May, yielded seven large branchiate tiger salamanders. Aquatic funnel trapping and seining efforts in 1996 yielded a total of 714 branchiate and 14 metamorphosed tiger salamanders, as follows: 5 large (>150 mm) branchiate salamanders were collected on 6 May; 42 branchiate salamanders and 2 partially metamorphosed salamanders were collected on 6 August; 38 branchiate salamanders were collected on 3 September; and 41 were collected on 6 September. Six traps checked on 7 September captured 567 branchiate animals. On this day, twenty additional branchiate animals were collected by seining. Pitfall traps checked on 29 August yielded 12 newly metamorphosed animals.

Color patterning.—Color patterning could not be used to distinguish cannibal morph from typical animals. Larvae and paedotypic animals have a background color ranging from olive to yellow, with olive tending dorsally, yellow ventrally and in some animals onto the opercular area. Of two cannibal morphs collected in September the larger was more brightly yellow. Darkly pigmented areas are superimposed on this ground color. These darker areas do not cross the dorsal midline, but extend down the flanks and usually across the venter. Dorsolateral pigment patterning varies across animals, and within animals between the trunk and the tail. Trunk pigmented regions were columnar or dumbbell shaped, interconnected and generally oriented dorsoventrally. On the tail, pigmented regions continued to be oriented dorsoventrally but bands tended to be both thicker and longer. Pigment patterning on the area dorsal to the hindlimbs was transitional. Patterning was generally similar but asymmetrical between sides of the animal.

This dorsolateral pigmentation pattern held for most animals. However, variations existed even among the relatively small number of animals (30) that were brought to Indiana and closely examined. Individuals exhibited a ground color that could be dark or light, and that varied in the extent of the area covered by pigment. Some animals had more numerous, smaller and more circular pigmented regions that again became dorsoventrally elongated on the tail. A few animals had yellow-gold pigment associated with their lateral line neuromasts. Two animals had a brighter yellow ground color with sharply delineated borders between the ground color and the pigment spots. One animal had circular pigment spots on its tail.

Ventral pigmentation patterns also varied. In general the ventral trunk contained transversely oriented pigment regions while the mandibular region contained rostrocaudally oriented pigmented regions. One animal had trunk pigment spots that did not extend onto its lateral ventral regions, but had a dark ventral midline stripe. Another animal had mid-ventral, transversely oriented ellipses.

Subspecies diagnosis.—Screening mtDNA with DGGE combined with color patterning and subspecies distributions was consistent with our initial subspecies diagnosis of *A. t. mavoritium* (Fig. 1). DGGE gels showed that these animals do not have *A. t. tigrinum* mtDNA. The mtDNA from *A. t. melanostictum*, *A. t. diaboli* and *A. t. mavoritium* cannot be differentiated using this technique. While the mtDNA fragment tested shows a high degree of variation between the eastern and western subspecies of tiger salamanders, there is a low degree of variation among western tiger salamander subspecies (E. Routman, pers. comm.).

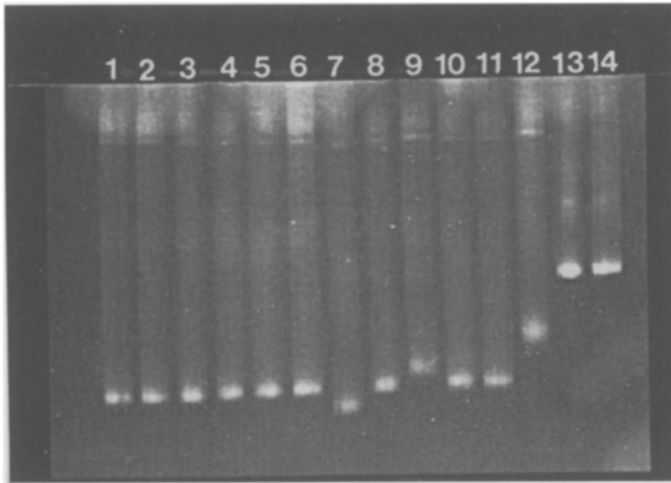


FIG. 1.—Denaturing gradient polyacrylamide gel showing electrophoretic migration variation in *A. tigrinum*. Lanes 1 and 2 are *A. t. diaboli* from near Jamestown, North Dakota; lanes 3–6 are *A. t. mavortium* from our study site near Brookings, South Dakota; lanes 7 and 8 are *A. t. melanostictum* from Cherry Co., Nebraska; lanes 9 and 10 are *A. t. mavortium* from Frontier Co., Nebraska; lanes 11 and 12 are *A. t. mavortium* from Valley Co., Nebraska; lane 13 is *A. t. tigrinum* from Dickinson Co., northwestern Iowa; lane 14 is from St. Louis Co., Missouri. The migration distances for the eastern (*A. t. tigrinum*) and western subspecies (all others) fall within two separate gel regions; the eastern subspecies always exhibits a much slower migrating fragment than the western subspecies (see text)

This diagnosis expands the known range of *A. t. mavortium* into South Dakota, 150 km north of its formerly recognized range.

Size distribution.—Sizes of animals varied seasonally (Fig. 2). Salamanders collected in May of both 1995 and 1996 were large branchiate animals (Fig. 2A). In the August 1996 sampling period, large animals were present, but a cohort of smaller animals (58–95 mm SVL) made up the majority of the individuals collected (Fig. 2B). During the final sampling period, September 1996, animals ranged in size between 51 and 130 mm SVL (Fig. 2C). The subset of animals collected in September 1996 and critically examined in Indiana ranged from 61–130 mm SVL (Fig. 2D). The two largest animals and one smaller animal were cannibal morphs (see below; Fig. 2).

Sex ratio and reproductive maturity.—Of the 24 animals collected in September 1996 and dissected to determine sex, 23 were males. In these animals, testis size, measured by taking the logarithm of the testis width midway along its rostrocaudal extent, was proportional to snout vent length. Histological analyses of gonads in four males (80, 100, 110, 125 mm SVLs) revealed primary spermatogonia (*cf.*, Armstrong, 1989; not shown here). The single female (135 mm SVL) in our sample had ovaries containing vitellogenic oocytes (Beetschen and Gautier, 1989) not shown here.

Morph diagnosis.—Cannibal morphs were rare, comprising only 4 of the 32 animals examined in the laboratory. At least two others exhibited an intermediate tooth hypertrophy. It is probable that other cannibals were present among the 714 branchiate animals collected in 1996 (six suspected cannibals sampled in August 1996 and many probable intermediates or cannibals sampled in September 1996 were released before MJL could verify morphotype). The diagnosis of cannibal morphs—1 collected in August and 3 of the largest pae-

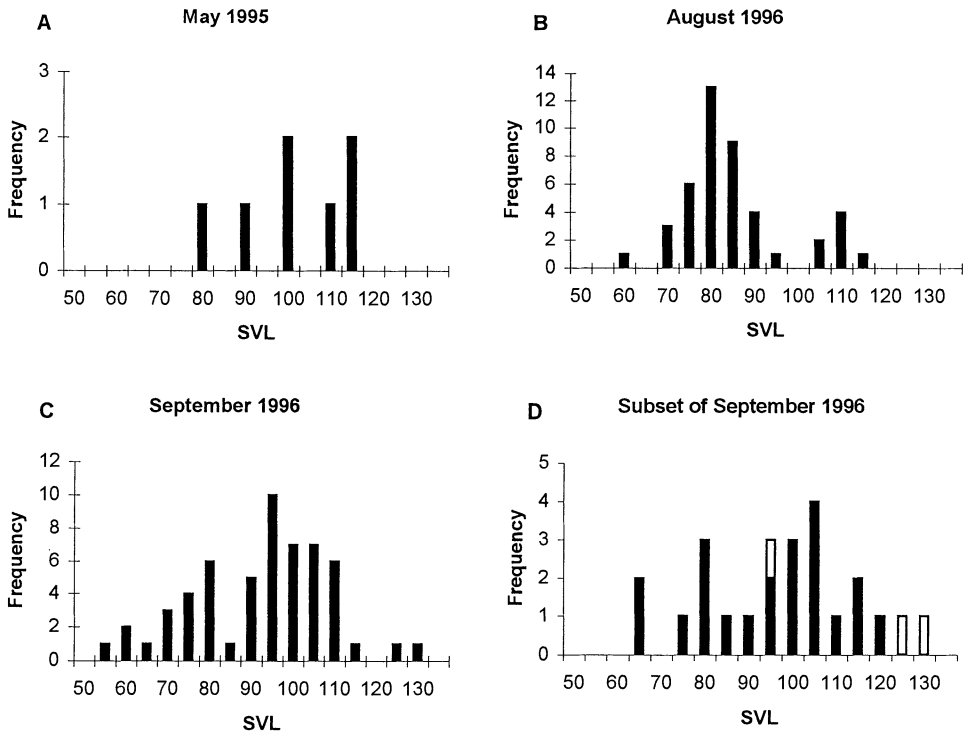


FIG. 2.—Sizes of *A. t. mavortium* varied seasonally. The salamanders collected in May of 1995 (A) were large branchiate animals. In August 1996, large animals were present, but a cohort of smaller animals (58–95 mm SVL) made up the majority of the animals collected (B). During September 1996, the majority of individuals in the population were between 70 and 110 mm SVL (C). Size distribution for a subsample of animals collected in September of 1996 and taken to Indiana for confirmation of morphotype. Cannibal morphs are indicated by light bars, noncannibal morphs by dark bars (D)

dotypic animals collected in September—was determined by qualitative head morphology and degree of vomerine, maxillary, premaxillary and dentary tooth hypertrophy. Both sexes were represented.

The tooth morphology varied among the three cannibal morphs examined (the fourth cannibal was maintained live and could not be fully examined). In the two males, teeth on the rostromedial vomerine tooth ridges appeared more hypertrophied than either teeth on the caudolateral vomerine ridges or on the maxillary, premaxillary, and dentary bones (Fig. 3A, B). While the large female cannibal morph exhibited hypertrophied teeth on the rostromedial vomerine tooth ridges, the caudolateral ridges were notably reduced, as were the teeth on these ridges, and the teeth on the maxillary, premaxillary and dentary bones (Fig. 3B). These smaller teeth represented a developmental endpoint, not a loss or damage resulting from injury or usage. In fact, in this same female, evidence of damage from injury was present; several teeth from the rostromedial portions of the rostromedial tooth ridges appeared to have been once present but had been sheared. The natural variation in hypertrophy of tooth ridges and in tooth size in cannibal morph *A. t. mavortium* differs from that seen in cannibal morph *A. t. tigrinum* from northwestern Iowa (Fig. 3C), which exhibit uniform tooth hypertrophy.

Of the six live branchiate salamanders observed in the laboratory, three metamorphosed between October and November. Two additional salamanders, one large cannibal and one first-year typical, metamorphosed in February. One large intermediate cannibal remained branchiated through May of 1997, when it was released back into Kneip Wetland.

Food habits.—In August, 1996, five of the six suspected cannibal morphs dissected in the field contained fathead minnow remains. The sixth suspected cannibal morph was preserved in the field and sent to Indiana where morphotype identification was confirmed. Dissection of this 95-mm, male, cannibal morph showed that the gut contained one conspecific (63 mm SVL) and three fathead minnows. In September 1996, gastric lavage on 56 suspected typical morphs revealed that only six animals had fathead minnows in their guts.

Skeletochronology.—Skeletochronology of the humeri of the three animals examined demonstrated first, that the cross sectional morphology of these branchiate animals consists of a thin bone layer surrounding a large lumen (marrow cavity); a morphology more similar to published photographs of larval animals than adults (Fig. 4A, C, E). Secondly, histology revealed that the thickness of bone cortex corresponded to the size of the animal (Fig. 4B, D, F). The animals with SVLs of 135, 120, and 95 mm had bone thicknesses of 200, 150 and 100 μm , respectively. Thirdly, skeletochronology demonstrated that the large female exhibited a partial lag line (Fig. 4B), indicating both that she was at least over 1-y-old (*i.e.*, she was not a young-of-the-year animal), and that asymmetrical bone resorption from the marrow cavity had occurred.

DISCUSSION

This population of *A. t. mavortium* includes animals that exhibit either the typical or cannibal morphology, and that may either metamorphose or remain paedotypic. We focus our discussion on the ecological and evolutionary implications of this finding.

Size distribution.—Size distributions of branchiate salamanders varied seasonally and demonstrate the variability of this subspecies. The large animals trapped in May of 1995 and 1996 represent branchiate animals that had overwintered. The absence of smaller animals from these samples indicates that either (1) young-of-the-year larvae were not yet present or (2) the larvae were too small to be captured by funnel traps. Small, newly metamorphosed animals captured in pit-fall traps in August 1996 confirm that some larvae metamorphose in their first year. The presence of both a large and a smaller cohort of animals in August and September of 1996 indicates multiple age classes of branchiate animals. The lag line on the humerus of the large gravid female collected in August 1996 (130 mm SVL) confirms that some animals remain as branchiates at least into their second year.

The variable life history observed in this population of *A. t. mavortium* is similar to that of populations of *A. t. diaboli* from central North Dakota described by Larson (1968), Buchli (1969) and Wiedenheft (1983). These populations include typical larvae that metamorphose in late summer and paedotypic animals that overwinter as branchiates. Most paedotypes metamorphose in their second summer when young of the year larvae became present. However, Buchli (1969) believed that some animals remained paedotypic for more than 2 yr. Both branchiate and metamorphosed young-of-the-year salamanders developed secondary sex characteristics and mature gonads between August and September (Weidenheft, 1983). Buchli (1969) noted that in the fall, both adult metamorphosed females and branchiate females developed eggs. However, eggs were not present in the branchiate females the following spring and he was unable to determine whether eggs were resorbed over the winter or laid under the ice. While in most years, branchiate animals were present year round, in some years branchiate animals were eliminated by winterkill (Buchli, 1969;

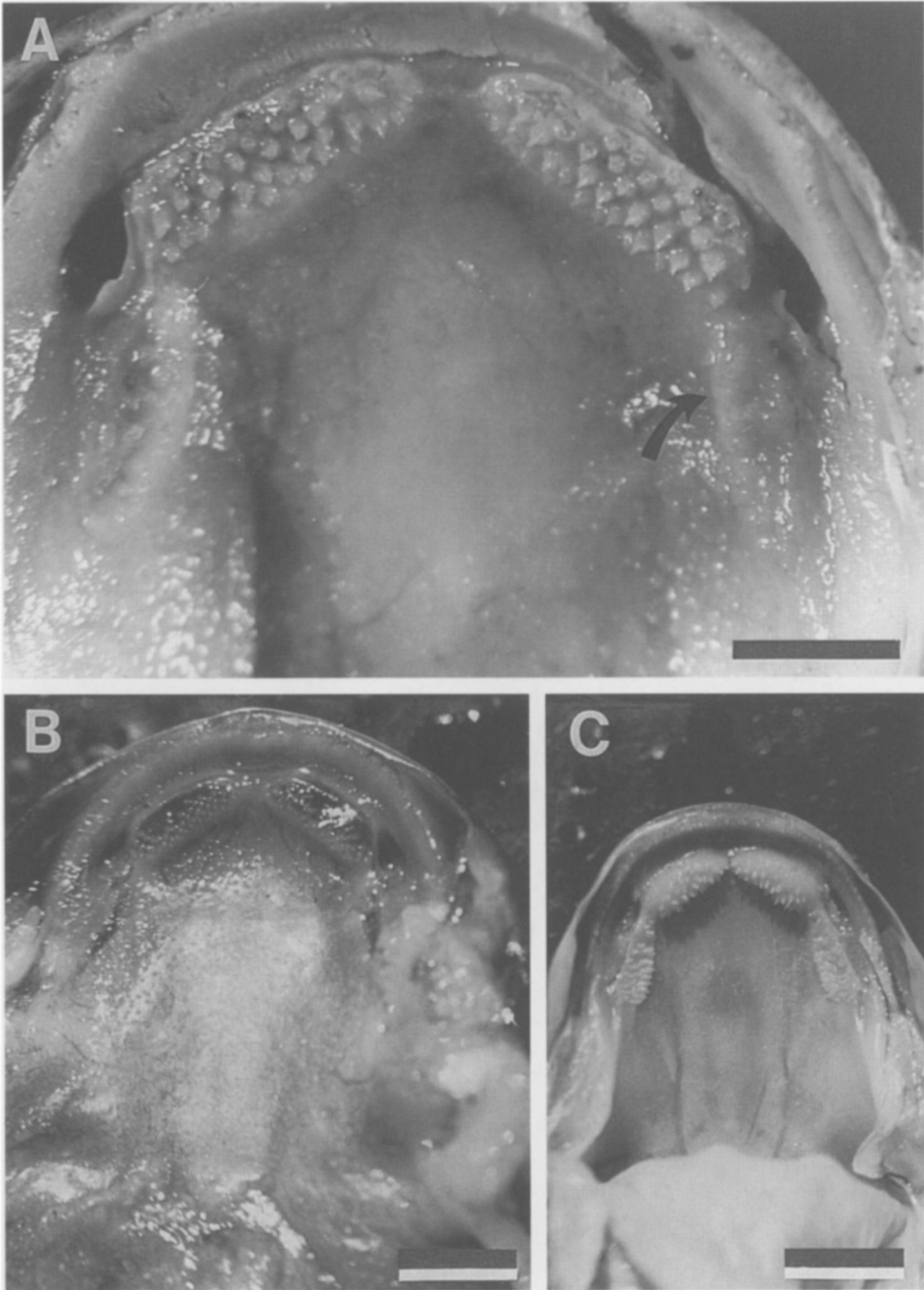


FIG. 3.—In both of the dissected *A. t. mavortium* cannibal morphs (A, B), teeth on the rostromedial vomerine tooth ridges exhibited more hypertrophy than the teeth on the caudolateral vomerine ridges (arrow in A) and on the maxillary, premaxillary, and dentary bones. For example, the large male (A) exhibited reduced caudolateral ridges, teeth on these ridges, and teeth on the maxillary, premaxillary

Wiedenheft, 1983). Buchli (1969) hypothesized that the variability in this population contributed to its survival.

Male biased sex ratio.—We have no explanation as to why 23 of the 24 animals whose gonads we examined were males. It may be that males are slower to metamorphose and therefore overwinter as branchiate animals. However, this explanation is not supported by the female biased sex ratio for *A. t. diaboli* reported by Buchli (1969) and Weidenheft (1983). Alternatively, it may be that males and females segregate ecologically and that males predominated at our sample site. Indeed, Norris (1989) showed a transient male bias in spring collections of paedotypic *A. t. mavortium* from Colorado. We do not know if gender influences morphotype in these animals. If there is a bias it is not obligate; the single female collected was both a paedotype and a cannibal morph.

Cannibal morphs.—Cannibal morphs were rare in our study population. Our results concur with Powers (1907) in at least three of his generalizations about cannibal morphs: (1) that the cannibal morph is rare; (2) that “when present it was not by itself, but only in small numbers among a great many ordinary individuals;” and (3) that “specimens of this type and even transitional forms approaching it only were always larger than the other larvae of the same year accompanying them, sometimes very much larger.”

The *A. t. mavortium* cannibal morphs described here exhibit a pattern of tooth hypertrophy that is different than the cannibal morph *A. t. tigrinum* described by Lannoo and Bachmann (1984), the nearest tiger salamander population where cannibal morphs have been described. In *A. t. tigrinum* cannibals, both the rostromedial and caudolateral vomerine tooth ridges are hypertrophied (Fig. 3C). In the three *A. t. mavortium* cannibals, the rostromedial vomerine teeth were enlarged, similar to the morphology in *A. t. tigrinum*, but the caudolateral vomerine teeth varied, and were usually smaller (e.g., Fig. 3A, B). If observations on additional animals confirm these suspicions, we predict that we could confidently assign cannibal morphs to either the Iowa (*A. t. tigrinum*) or South Dakota (*A. t. mavortium*) populations based solely on vomerine tooth morphology.

Paedotypic animals.—Paedotypic tiger salamanders are defined as sexually mature animals in branchiate bodies (e.g., Gould, 1977). Here, we demonstrate paedotyposis through a combination of gonadal morphology and skeletochronology. The testes of the largest males were enlarged; histology revealed primary spermatocytes. The large female in our collection exhibited darkly pigmented ovaries, resembling that of post-breeding hynobiids in winter, as described by Hasumi (1996). The size of the ovaries (700 μm) is comparable to that of *A. mexicanum* undergoing vitellogenesis (Beetschen and Gautier, 1989). In the large female in our sample, skeletochronology revealed portions of one lag line, suggesting that she was at least in her second summer.

Note that we do not use skeletochronology here to establish age estimates. The large marrow cavities exhibited by these paedotypic animals suggest that substantial bone resorption occurs. This suspicion is confirmed by noting that the lag line observed in the large female had been partially resorbed. Instead we use skeletochronology to show that some animals in this population persist as paedotypic animals through their second summer, as was suspected of paedotypic *A. t. diaboli* by Buchli (1969). In demonstrating this, we elim-

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and dentary bones. The cannibal morph female (B) also exhibited smaller teeth on the caudolateral vomerine, maxillary, premaxillary and dentary tooth ridges. This pattern of tooth morphology in *A. t. mavortium* differed from that seen in *A. t. tigrinum* from northwestern Iowa (C), where full tooth hypertrophy is characteristic. Scale bars = 0.5 cm (A); 1 cm (B, C)

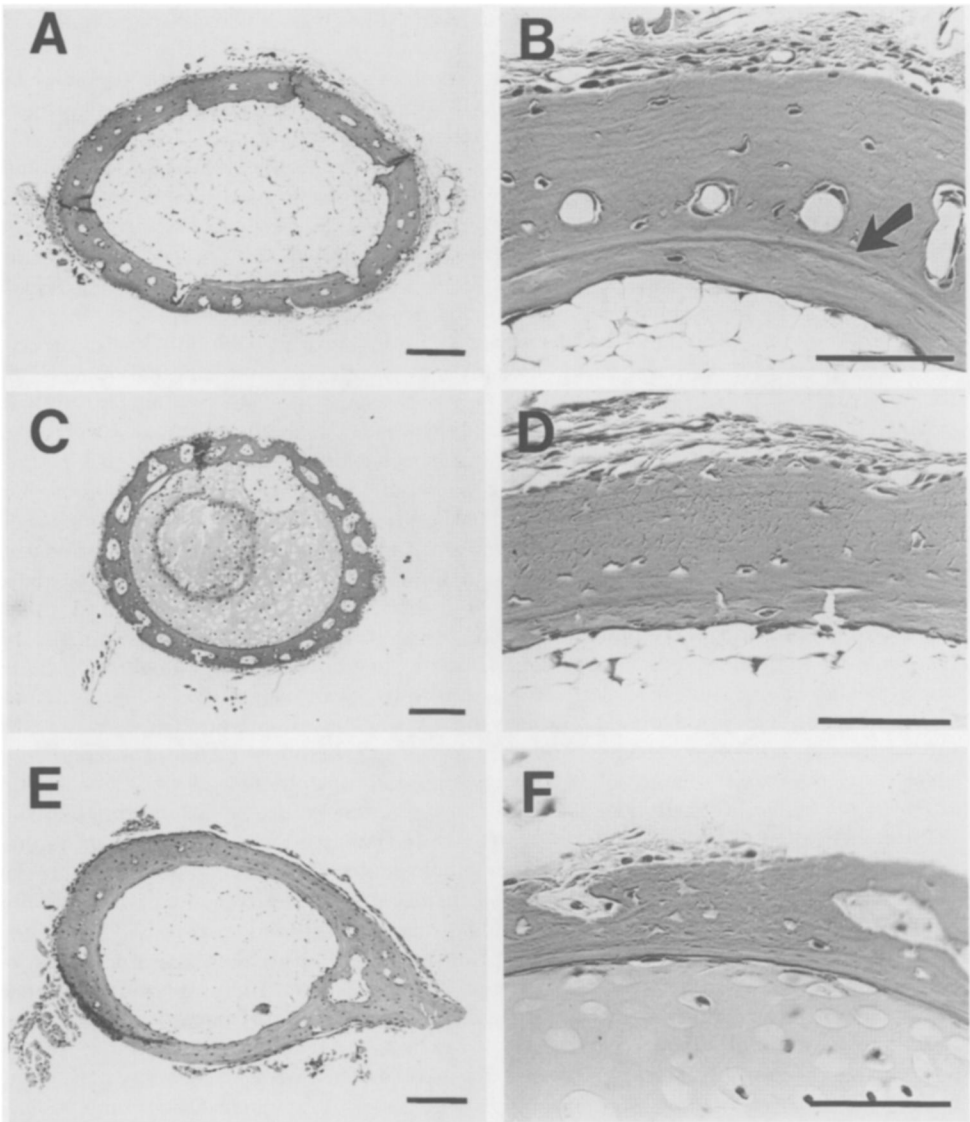


FIG. 4.—Skeletochronological analysis of *A. t. mavortium* from Kneip Wetland. A, B) a 135 mm SVL cannibal morph female; C, D) a 120 mm SVL intermediate cannibal morph male; E, F) a 95 mm SVL cannibal morph male. In these branchiate *A. t. mavortium* note the large size of the marrow cavity (A, C, E). Note also that the thickness of bone cortex (B, D, F) corresponded to the size of the animal. The large female (A, B) exhibited a partial lag line (B; arrowhead). Scale bars = 200 μm (A, C, E) and 200 μm (B, D, F)

inate the possibility that all animals develop gonads during their first fall but metamorphose before breeding the following spring (e.g., as Wiedenheft, 1983 reports for *A. t. diaboli*; such animals could not be considered true paedotypes). We also eliminate the possibility that all animals first breed as paedotypes then metamorphose, as has been reported for *A. t. mavortium* (Powers, 1907) and *A. talpoideum* (Patterson, 1978; Semlitsch, 1985, 1987; Semlitsch and Wilbur, 1989; Semlitsch *et al.*, 1990; Scott, 1993; Whiteman, 1994). Consistent with our conclusion, Powers (1907) observed one paedomorph that had not yet metamorphosed after three years of observation.

Cannibal morphs and paedotypes.—We suggest as a working hypothesis that the paedotypic and cannibal morph phenotypes are not genetically linked and sort independently. Observations that cannibal morphs are slow to metamorphose (Powers, 1907; Rose and Armentrout, 1976) could indicate that paedotypic and cannibal morph phenotypes are in fact linked, which would negate our hypothesis of independent assortment. Lannoo *et al.* (1989, 1990) have shown that cannibal morph *A. t. tigrinum* are among the first to metamorphose, although these observations were from animals in a population that does not exhibit paedotyposis.

The history of Kneip Wetland and implications for A. tigrinum morphotypes.—The fall and winter of 1990 was probably the first time in at least 70 y that the restored Kneip Wetland held water long enough to support amphibian reproduction. There are two consequences to this history. First, it sets an upper limit on the age of paedotypic tiger salamanders—1996 would have been the sixth year of water, so animals could not have been more than 5-y-old (see Glass, 1951). Secondly, it implies that salamanders either imported a genetic predisposition for the cannibal morphotype as they recolonized this wetland, or that this morphotype arose on site, perhaps in response to a unique combination of environmental factors present in this wetland (we explore this possibility further below). We believe that the first scenario is the most likely. Cannibal morphs were first described in *A. t. mavortium* (Powers, 1907) and are known to occur regularly in this subspecies (Dunn, 1940; Collins and Cheek, 1983). Yet, extensive sampling done in natural wetlands surrounding the study site has so far failed to yield other cannibal morphs, an observation that supports the second scenario. Perhaps the reason cannibal morphs are expressed in Kneip Wetland and not surrounding wetlands is that alone among wetlands in this region, environmental conditions in Kneip favor this phenotype.

The 1996 *A. t. mavortium* population at Kneip Wetland resembled the profile of morphotypes described by Powers (1907). Paedotypic animals consisting of both typical and cannibal morphs were present throughout the year. Young-of-the-year larvae were present during the summer, but by September these salamanders had either metamorphosed or were continuing to grow as branchiate animals. Indeed, it is likely that the paedotypic cannibal morphs we observed developed this morphology as larvae. Although no cannibal larvae were collected earlier in the summer of 1996 (see above), the 95 mm SVL male collected on 7 September may have been a first year animal.

Our study site may provide an excellent opportunity to examine subspecific morphologies in the context of shared ecological factors. Tiger salamander subspecies are known to vary in their tendencies to exhibit particular phenotypes (Dunn, 1940; Stebbins 1985; Conant and Collins, 1991). For example, *A. t. mavortium*, *A. melanosticum* and *A. t. diaboli* populations across their range are known to contain paedotypic animals. On the other hand, *A. t. tigrinum* contains only a few populations with paedotypic animals (Michigan [Collins *et al.*, 1980], Florida [Powers, 1907], southern Illinois [Brandon and Bremer, 1967], and central Iowa [MJL, animals collected at Ledges State Park, Boone Co., Iowa, 1980]). Subspecies tendencies towards the expression of cannibal morphs also vary. Cannibal morphs are

known from *A. t. mavortium*, *A. t. nebulosum*, *A. t. stebbensi*, *A. t. tigrinum* and *A. t. melanosticum* but not *A. t. diaboli* or *A. t. californiense*.

Distributions of paedotypic and cannibal morph animals: adaptations or historical contingencies?—The important question arises, is the subspecific predisposition to paedotyposis and/or cannibal morphs beneficial in the Great Plains? That is: (1) are cannibal morph, but not paedotypic phenotypes (*A. t. tigrinum*), uniquely successful in the southeastern region of the upper Great Plains (northwestern Iowa); (2) are paedotypic phenotypes, but not cannibal morphs (*A. t. diaboli* and *A. t. melanosticum*), uniquely successful in the central upper and western Great Plains (around Jamestown, North Dakota); and (3) is the combination of paedotypes and cannibal morphs (*A. t. mavortium*) successful in intermediate geographic regions (e.g., around Brookings)? If (3) is answered affirmatively, two possibilities exist for the presence of these phenotypes in our South Dakota study population: either they were brought in postglacially by colonizing animals during the past 12,000 years, or they arose de novo in response to local conditions (a true adaptation).

The advantages of paedotyposis in regions with a harsh terrestrial climate have been discussed (Snyder, 1956; Webb, 1969; Webb and Roueche, 1971; Sprules, 1974; Licht, 1992). These advantages are magnified in regions where aquatic conditions (frequent hypoxia and periodic drying) discourage the establishment of predatory fishes (Lannoo, 1996, 1998). Precipitation varies across the Great Plains, with moisture increasing from west to east. Low precipitation may create harsher terrestrial conditions for adult amphibians and therefore favor paedotypic animals. However aquatic habitats in these areas also dry during periodic droughts, which threatens paedotypic animals. Metamorphosis offers an escape from drying aquatic habitats, although it appears that the ability to metamorphose varies between larvae and paedotypic animals, and perhaps within paedotypic animals by age (Powers, 1907; Rose and Armentrout, 1976).

The advantages of cannibal morphs (rapid growth and large size) have also been discussed (Rose and Armentrout, 1976; Collins *et al.*, 1980; Lannoo and Bachmann, 1984; Lannoo *et al.*, 1990). From this discourse it is not apparent why this phenotype should be uniquely favored in arid regions. The advantages of cannibal morphs would appear to be lost in seasonal wetlands if cannibal morphs are slow to metamorphose and these wetlands dry (Powers, 1907; Rose and Armentrout, 1976; Lannoo and Bachmann, 1984). Lannoo *et al.* (1989, 1990) report that cannibal morphs are among the first to metamorphose, which would be an advantage. If such an advantage indeed exists, it would also seem to be favorable in the seasonal basins of more mesic regions.

Multiple origins of cannibal morphs.—Cannibal morphs may be phenotypes that are relatively easily achieved both developmentally and evolutionarily. In addition to its presence in the four tiger salamander subspecies, cannibal morphs have been reported from another North American ambystomatid (*A. macrodactylum*; Walls, 1993a, b) and an Asiatic hynobiid, *Hynobius retardus* (Wakahara, 1995; Nishihara, 1996). It is likely therefore that this phyletic distribution of cannibal morphs represents at least three separate derivations.

The difference in degree of tooth hypertrophy between the rostromedial and caudolateral vomerine tooth ridges between *A. t. tigrinum* and *A. t. mavortium* (Fig. 3) suggests either separate derivations or a subsequent modification of the common ancestral morphology. One scenario for the presence of cannibal morphs in this western population of *A. t. tigrinum*, but not in eastern populations (Lannoo *et al.*, 1989), is the transfer of genes through hybridization with *A. t. mavortium*. Indeed, the landscape where the *A. t. tigrinum* cannibal morph occurs, unlike much of the upper Great Plains, has only recently been deglaciated (ca. 12,500 y ago). These animals therefore must have immigrated from either the southern or western unglaciated regions. If animals originated from the west, they may

have acquired the genetic capacity for the cannibal morphology from *A. t. mavortium* populations. As attractive as this scenario appears, it has not been confirmed through genetic analyses, does not explain the induction of cannibal morphs from Indiana populations, and does not appear to be supported by the differences in tooth morphology observed between these two subspecies.

Cannibal morphs and "paedocannibal" morphs.—We propose that a formal nomenclatural distinction be considered between cannibal morphs in larval animals and cannibal morphs in paedotypic animals. Certainly the rationale for distinguishing between these morphs in typical animals can be extended to cannibal morphs. Paedotypic cannibal morphs exhibit a life history pattern distinct from metamorphic cannibal morphs, and these differences have adaptive consequences. In his original description of cannibal morphs, Powers (1907) noted that this morphology occurs in both larvae and paedotypic animals. Rose and Armentrout (1976) define cannibal morphs as a subset of potential adult morphologies, while the experiments and observations of Collins (1981), Collins and Cheek (1983), Pfennig and Collins (1993), and Pfennig *et al.* (1991) demonstrate that this morphology can arise in larvae. Lannoo and Bachmann (1984) noted only *A. t. tigrinum* cannibal morph larvae; adults in their study population are terrestrial. To open this debate, we suggest that the term cannibal morph be retained for the larval form, and that the term "paedocannibal morph" be applied to animals that exhibit both paedotypic and cannibal morph phenotypes.

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