

Timing of Reproduction of Paedomorphic and Metamorphic *Ambystoma talpoideum*

DAVID E. SCOTT

Savannah River Ecology Laboratory, Drawer E, Aiken, South Carolina 29802

ABSTRACT.—Facultative paedomorphosis in salamanders is a plastic trait that may represent an adaptation to fluctuating environmental conditions. I compared the timing of reproduction in paedomorphic and terrestrial-morph *Ambystoma talpoideum* at the same pond. Paedomorphic adults laid eggs approximately 6 wk earlier than terrestrial morphs. Early egg-laying and subsequent growth of hatchlings resulted in a significant size advantage for larvae from paedomorphic parents at the time that terrestrial-morph eggs hatched. These observations suggest that, under certain environmental conditions, facultative paedomorphosis is advantageous.

INTRODUCTION

The generalized life cycle of amphibians consists of an aquatic larval stage followed by metamorphosis to a terrestrial juvenile and then adult stage in which reproduction occurs. In salamanders of the genus *Ambystoma*, however, many species exhibit "paedomorphosis" in which larval morphology is retained in reproductive (aquatic) adults (Sprules, 1974; Gould, 1977). Although some species are obligately paedomorphic (e.g., *Ambystoma mexicanum*), others are facultatively paedomorphic and retain the ability to metamorphose (Semlitsch and Wilbur, 1989). The causes of facultative paedomorphosis remain largely unknown (Harris, 1987).

The developmental plasticity inherent in facultative paedomorphosis may be an adaptation to fluctuating environmental conditions and selection pressures (Harris, 1987). The potential for alternate developmental paths enables individuals to respond to differences in opportunities for growth between aquatic and terrestrial environments (Wilbur and Collins, 1973). For example, *Ambystoma talpoideum* (the mole salamander) is a facultatively paedomorphic species (Patterson, 1978; Semlitsch, 1987a) that breeds in temporary ponds in the southeastern U.S. (Conant and Collins, 1991). Paedomorphic and metamorphic adults can coexist in the same pond (Semlitsch, 1985; Semlitsch and Gibbons, 1985), but among-pond variation in hydrologic regime may promote differences among populations in the proportion of paedomorphic individuals. In general, the metamorphic phenotype predominates in temporary ponds that dry in most years, and the paedomorphic phenotype predominates in nearly permanent, fish-free ponds (Semlitsch and Gibbons, 1985; Semlitsch *et al.*, 1990). In *A. talpoideum*, facultative paedomorphosis has a genetic basis that can be altered by natural selection (Semlitsch and Gibbons, 1985; Harris, 1987; Semlitsch and Wilbur, 1989). An individual's propensity to metamorphose, or ability to assess the severity of aquatic conditions, is considered the trait under selection (Semlitsch *et al.*, 1990; Harris *et al.*, 1990).

Little is known concerning the relative advantages and disadvantages of facultative paedomorphosis. Within a population, temporal variation in selection pressure may maintain plasticity in the propensity to metamorphose (Semlitsch *et al.*, 1990), if selection has not been persistent enough to eliminate either morph. In years when a pond dried, there may be a selective cost incurred by facultative paedomorphs that are forced to metamorphose. Semlitsch *et al.* (1988) reported that individual *Ambystoma talpoideum* that delayed metamorphosis until their pond almost dried subsequently attained smaller adult body size relative to individuals that metamorphosed earlier at high water levels. Several studies have docu-

mented a relationship between adult body size and traits related to fitness in amphibians (e.g., Salthe, 1969; Howard, 1980). The late-metamorphosing individuals, if they represented "likely" paedomorphs, may be at a selective disadvantage under these conditions.

When a pond does not dry, facultative paedomorphosis may be favored. Survival and growth rates may be higher in the aquatic than in the terrestrial environment (Semlitsch, 1985). One-yr-old paedomorphic *Ambystoma talpoideum* have a larger body mass than 1-yr-old metamorphs of the same snout-vent length (SVL; Semlitsch, 1985), perhaps indicating better growth under aquatic conditions. However, Semlitsch (1985) also noted that 1-yr-old terrestrial morphs exhibited longer SVL and produced more eggs than 1-yr-old paedomorphs.

Both terrestrial morphs and paedomorphs can mature in 1 yr, but there may be selection for paedomorphosis if paedomorphs reproduce earlier than metamorphs (Semlitsch, 1985; Semlitsch *et al.*, 1990). Early egg-laying, hatching and larval growth may result in larvae that have a competitive advantage over larvae of terrestrial morphs, and that can better escape from gape-limited predators (Wilbur, 1980). Basically there is much speculation, but few data, concerning the relative costs and benefits of facultative paedomorphosis. Consequently, I examined the within-season differences in oviposition date and larval body size between paedomorphic and metamorphic parents in *Ambystoma talpoideum* to enable a better assessment of the possible selective advantages of facultative paedomorphosis.

METHODS

Observations on the timing of egg-laying were made at Ginger's Bay (GB), a 0.8-ha Carolina bay located in a sandhills habitat on the U.S. Department of Energy's Savannah River Site in Aiken County, South Carolina. Carolina bays are shallow, elliptical depressions located on the Atlantic Coastal Plain of parts of the southeastern United States. Many Carolina bays are temporary ponds and typically fill with rain in late autumn or early winter and dry in late spring or summer (Sharitz and Gibbons, 1982). Bays serve as important breeding sites for many species of amphibians (Pechmann *et al.*, 1991). Ginger's Bay supports large populations of *Ambystoma opacum* and *A. talpoideum*. More detailed site descriptions may be found in Jackson *et al.* (1989) and Scott (1990).

The dates of pond-filling and drying at GB have been recorded since the summer of 1984. Ginger's Bay dried each spring or summer during 1984–1990, but did not dry in the summer of 1991. Experiments in artificial ponds that used adult *Ambystoma talpoideum* from the GB population indicated a relatively high incidence of paedomorphosis compared to nearby populations. The prevalence of paedomorphs suggests that the recent drying history of GB is not indicative of its long-term hydrologic regime (Semlitsch *et al.*, 1990; Harris *et al.*, 1990).

In October 1991 aquatic sampling revealed that many larvae from the previous winter had remained in GB and had become sexually mature (i.e., paedomorphic). Over 100 individuals were captured with dip nets and minnow traps, and all appeared to be mature, as determined by swollen cloacal glands in males and enlarged eggs in females. Four "suspected" female paedomorphs were killed and dissected, and had yolk-filled follicles.

In order to keep paedomorphs separated from metamorphic adults that would migrate to the bay beginning in December, I placed approximately 20 male and 28 female paedomorphs of *Ambystoma talpoideum* into each of three field enclosures (41 m²; see Scott, 1990, for details on enclosure design) during 8–18 October 1991. No metamorphic *A. talpoideum* were present in these pens because metamorphic adults had not yet migrated into GB, and all pens had been flooded continuously since October 1990. After being stocked with paedomorphs, the pens were checked weekly for eggs and hatchlings. Metamorphic adults that

returned to breed in GB were captured in 20-liter pitfall traps at a drift fence that encircled the breeding site (Gibbons and Semlitsch, 1981). Twenty males and females from the first major pulse (2 January 1992) of incoming females were confined to two 1.5-m diam plastic wading pools that were placed in 30 cm of water in GB. Leaf litter was added to each pool to cover the bottom and provide natural substrate for egg deposition, and pools were filled with pond water and covered with screen to prevent adults from escaping. Previous experiments had shown that adults readily oviposited within 1 wk in similar artificial pools, and by using the wading pools I was able to isolate metamorphic and paedomorphic adults. After introduction of the adults, pools were checked every 3rd day for eggs and hatchlings.

After the hatching of eggs from metamorphic parents on 18 February 1992, 20 larvae from both parental morphs were captured, measured to the nearest 0.5 mm total length (TL), and released. Body-size values in the text represent group means \pm 1 standard error ($\bar{x} \pm 1$ SE). Group means were compared using the t-test procedure of the Statistical Analysis System (SAS Institute, 1985).

RESULTS

In the enclosures with only paedomorphic *Ambystoma talpoideum*, well-developed eggs were discovered on 15 December 1991. The more advanced eggs were at Harrison embryonic stages 25–30 (Rugh, 1962), and probably were laid in late November. By 24 December all three enclosures contained large numbers of eggs from the paedomorphic adults. By 31 December, newly hatched larvae were found in all three enclosures.

Metamorphic male *Ambystoma talpoideum* ($n = 93$) began to enter GB on the night of 17 December; the first females ($n = 24$) on 23 December. Additional females migrated into GB on 29 December 1991 ($n = 4$), 2 January 1992 ($n = 121$), 13 January 1992 ($n = 260$), and 27 January 1992 ($n = 8$). Twenty pairs of females and males from 2 January were placed in wading pools on 3 January 1992. Newly deposited eggs (pre-Harrison stage 6) were discovered in the pools on 11 January 1992. The first hatchlings appeared in wading pools on 18 February 1992. Hatchlings from metamorphic parents averaged 8.8 ± 0.2 mm total length ($n = 20$). At this time the larvae from paedomorphic parents were significantly larger ($t = 11.59$, $df = 38$, $P < 0.0001$), at 17.1 ± 0.7 mm total length ($n = 20$).

DISCUSSION

Paedomorphic *Ambystoma talpoideum* oviposited much earlier than their metamorphic counterparts during this study. Metamorphic females did not begin to enter GB until a week after well-developed eggs from paedomorphic parents were observed. Earlier egg-laying resulted in earlier (by 6 wk) hatching of offspring from paedomorphic adults, which resulted in a larval body-size difference. After the eggs from metamorphic adults hatched, the larvae from the two parental morphs could not be maintained under comparable conditions. Consequently, because the growth rates of both groups were not measured throughout the larval period, I do not know whether the initial size difference was maintained.

Body size differences in larval salamanders may influence foraging opportunities and growth rates. For larval *Ambystoma opacum* under purely exploitative competition for small prey, larger larvae are not necessarily superior competitors; however, physical interactions with larger conspecifics may reduce the growth rate of smaller larvae (Smith, 1990). Aggressive superiority is associated with larger body size in both *A. talpoideum* and *A. maculatum* (Walls and Semlitsch, 1991). In aggressive interactions between two larvae, the difference in size between “winners” and “losers” was correlated with a corresponding foraging advantage in winners (Walls and Semlitsch, 1991). The importance and prevalence of physical interactions under field conditions is unknown.

Earlier hatching and larger body size in the larvae from paedomorphic adults also may reduce mortality from predators. Numerous predaceous amphibian and invertebrate species inhabit Carolina bays, and the early hatching *Ambystoma talpoideum* may incur lower predation from these species than late hatching larvae. Larval *A. opacum* are numerous in Ginger's Bay, and at the time of hatching of eggs from metamorphic adults of *A. talpoideum*, larval *A. opacum* averaged 22.9 ± 0.3 mm total length ($n = 20$). Predation by larval *A. opacum* on larval *A. maculatum* increased as the relative size differences between the species increased (Stenhouse *et al.*, 1983). Adult red-spotted newts (*Notophthalmus viridescens*) also occur at GB at low densities, and predation intensity by newts is also related to body size (Morin *et al.*, 1983; Alford, 1989).

Predation on amphibian larvae by immature odonates generally decreases as tadpole size increases (Heyer *et al.*, 1975; Caldwell *et al.*, 1980; Brodie and Formanowicz, 1983; Travis *et al.*, 1985), as size of the odonate naiad decreases (Travis *et al.*, 1985), and as odonate density decreases. Benke (1969) noted that individuals of several dragonfly species that overwinter in permanent ponds on the Savannah River Site grow slightly in late autumn and early winter, and reach lowest population densities by midwinter. These conditions may mean that hatchlings from paedomorphic parents are exposed to smaller, earlier instar odonate naiads, possibly at lower densities, than the late hatching larvae from metamorphic parents. In early spring, as odonate eggs hatch and naiad densities increase, late hatching salamander larvae may be more susceptible to predation.

Pond drying is also an important source of mortality in amphibians (*e.g.*, Shoop, 1974; Semlitsch, 1987b; Pechmann *et al.*, 1989). Regular, yearly pond drying favors metamorphosing individuals and selects against paedomorphosis. Occasional early pond drying may favor larvae from paedomorphic parents, however, if these larvae have a greater likelihood of achieving the minimum body size necessary for metamorphosis (Wilbur and Collins, 1973) before the pond dries.

The differences I observed between paedomorphic and metamorphic adults in the timing of reproduction may not be uncommon. Although pond permanency occurred in only 1 of 8 yr at Ginger's Bay, it is a more common occurrence at other Carolina bays (Sharitz and Gibbons, 1982). Also, it is likely that the hydroperiod record at GB (1984–1991) is from a period of unusually dry years (Pechmann *et al.*, 1991). These observations suggest that paedomorphic *Ambystoma talpoideum* have frequent opportunities for earlier reproduction, and may have a selective advantage under certain conditions.

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