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Hatching asynchrony, survival, and the fitness of alternative adult morphs in *Ambystoma talpoideum*

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Abstract

The mole salamander, *Ambystoma talpoideum*, exhibits both aquatic (gilled) and terrestrial (metamorphosed) adult morphologies. Previous studies have shown the existence of body-size advantages associated with the terrestrial morph in *A. talpoideum* and other polymorphic salamanders (e.g., *A. tigrinum*). However, aquatic adult *A. talpoideum* mature at a younger age and often breed earlier than terrestrial adults. We tested the hypothesis that early maturation and reproduction in aquatic adults increase fitness (irrespective of body size). We reared larval *A. talpoideum* in mesocosms and varied the timing of hatching, with early-hatching larvae representing the offspring from early-breeding aquatic adults, and late-hatching larvae representing the offspring of later-breeding terrestrial adults. Our results demonstrate significantly higher survival rates among early-hatchlings relative to late-hatching conspecifics, supporting the hypothesis that early reproduction may be an important mechanism mediating the polymorphism in *A. talpoideum*. We discuss our results within the context of size-based models of the fitness of alternative life-cycles.

Keywords Life-cycle polymorphism, Intraspecific priority effects, Metamorphosis, Paedomorphosis

Introduction

The timing of breeding is a critical consideration for organisms with spatio-temporally variable reproduction (Lack 1954). Whereas spatial variation in reproduction is a matter of interactions among populations or subpopulations, the effects of temporal variation are frequently a matter of direct inter- or intraspecific interactions. For example, temporal variation in reproductive activity may regulate community dynamics through predator-prey relationships (e.g., Fauth 1990; Fauth and Resetarits 1991) or interspecific competition (e.g., Ishii and Higashi 2001). The effects of reproductive asynchrony on populations (e.g., Olsson and Shine 1997) and intra-familial competition (reviewed by Krebs 1999) can be substantial as well.

In amphibians that breed in temporally variable habitats, breeding and hatching asynchronies frequently result in priority effects that structure communities, with early breeders generally having a competitive or predatory advantage over late breeders (e.g., Lawler and Morin 1993; Blaustein and Margalit 1994, 1996; Boone et al. 2002; but see Harris 1980). For many species that utilize seasonal wetlands as nuptial-natal sites, breeding in the population is synchronous and coincident with pond-filling, thus reducing or eliminating intraspecific priority effects. Consequently, the outcome of competitive interactions between asynchronously breeding species have been the subject of long-term field studies (e.g., Semlitsch et al. 1996) and experimental manipulations (e.g., Alford and Wilbur 1985; Wilbur and Alford 1985; Morin 1987; Morin et al. 1990). The importance of hatching asynchrony within amphibian populations remains poorly understood, however.

The mole salamander, *Ambystoma talpoideum*, exhibits substantial within-population variation in the timing of breeding and hatching. The breeding season extends from October to March (Petranka 1998), and like most other amphibians, metamorphosed adult *A. talpoideum* depend upon environmental conditions to signal the onset of the breeding season and to permit overland migration to breeding sites (Semlitsch and Ryan 1998). Unlike most other amphibians, however, *A. talpoideum* exhibits a life-cycle polymorphism (Patterson 1978) with aquatic, gilled adults (sometimes referred to as paedomorphs) foregoing the metamorphosis that results in transformed terrestrial adults. These aquatic adults are at the breeding grounds when they reach sexual maturity and may breed substantially earlier than terrestrial adults whose migration is limited by appropriate weather conditions (Krenz and Sever 1995). In some cases, the offspring from aquatic adults may hatch before metamorphic adults even begin to breed (Scott 1993).

The growth advantages afforded by early hatching can be critical, especially when growth, development, and survival are density-dependent, and inter- and intraspecific competition is potentially high, such as with ambystomatid salamanders (Semlitsch and Reichling 1989; Scott 1990; Boone et al. 2002). Aquatic adults mature at a significantly younger age than metamorphic adults of the same cohort (Ryan and Semlitsch 1998), with earlier reproduction (Krenz and Sever 1995) and hatching (Scott 1993) as potential consequences. Ryan and Semlitsch (1998) hypothesized that early maturation and breeding may confer a substantial fitness advantage to aquatic adults relative to metamorphs, manifested as increased survival and maturation of their offspring, and possibly larger size at metamorphosis. We tested this hypothesis by manipulating

hatching times of *A. talpoideum* reared in mesocosms (artificial ponds) to simulate asynchronous breeding of branchiate (early) and metamorphic (late) adults.

Materials and methods

We assessed the effects of hatching asynchrony in *A. talpoideum* by adding larvae to mesocosms at different times and densities. In order to unambiguously identify individuals that were added at different times, we used two genetically distinct families (“A” and “B”, see below). The timing of addition was either asynchronous, with individuals of each family added on “early” and “late” hatching dates approximately 40 days apart, or synchronous, with the simultaneous addition of both families at either the early or late addition date. The difference in the timing of hatching is fairly conservative. For example, Krenz and Sever (1995) found that branchiate females oviposited as early as 31 October one year, whereas the majority (77%) of metamorphic females did not even arrive at the same pond to breed until more than 70 days later. Because intraspecific competition is a variable and important factor in larval *A. talpoideum* populations in nature (e.g., Semlitsch et al. 1996), we tested each of the timing combinations at low (n=16 individuals) and high (n=32 individuals) density. Density manipulations as a means of controlling per capita resource availability in previous *A. talpoideum* mesocosm experiments have produced results compatible with those observed in nature (e.g., see density effects in Semlitsch 1987a, b; Ryan and Semlitsch 1998). Therefore, we had a fully-crossed three-factor design: two asynchronous treatments (A early/B late and B early/A late), two synchronous treatments (A early/B early and A late/B late), each at low and high densities, with four replicate mesocosms for each ($2 \times 2 \times 2 \times 4 = 32$ mesocosms).

We used genetic markers to distinguish between the families in the experiment (see below), and thus we had to ensure that the parental stock consisted of non-mated adults in breeding condition. This necessitated the use of terrestrial rather than aquatic adults for the parental stock, as aquatic adults can mate and store sperm prior to oviposition (Krenz and Sever 1995) but terrestrial adults do not mate until they reach the breeding ponds. The expression of the polymorphism in *A. talpoideum* is determined by both genetic and environmental factors (Semlitsch and Wilbur 1989; Semlitsch et al. 1990), and the use of one adult morph or the other as parental stock does not limit or significantly affect the expression of the full range of phenotypes (Semlitsch and Gibbons 1985; Semlitsch and Wilbur 1989; Semlitsch et al. 1990; Ryan and Semlitsch 1998, 2003). We used a drift fence coupled with 20-l pitfall buckets encircling Dry Bay (Aiken County, S.C.) to intercept adult *A. talpoideum* during breeding migrations on 26 November and 6 December 1999. Dry Bay is a 5-ha Carolina bay that dries infrequently (about once every 15 years) and has a large proportion of aquatic adults (T.J. Ryan, unpublished data). Adults in breeding condition (males with swollen cloacae and gravid females) were transported to the laboratory, where each was maintained individually in a polystyrene shoebox with moist paper towels (changed weekly) at 15°C.

We identified individuals for each breeding family using the malate dehydrogenase allozyme locus (Mdh, E.C. 1.1.1.37). Mdh in the Dry Bay *A. talpoideum* population has two alleles that occur at approximate frequencies of 0.4 and 0.6, so each breeding family was composed of individuals homozygous at one Mdh allele or the other. Because Mdh in this population conforms to Hardy-Weinberg equilibrium expectations (G.R. Plague, unpublished data), it is not under overt selection and therefore is presumably a neutral marker. Tail tips (~8 mm) from 102 individuals were

homogenized in 50 μ l crushing buffer (1 mg NADP, 10 μ l 2-mercaptoethanol, 10 ml diH₂O). Electrophoresis was performed on cellulose acetate plates as described in Hebert and Beaton (1993). All gels were run in a continuous 0.01 M citrate-phosphate buffer, pH=6.4 at 200 V for 45 min and stained with the recipe from Hebert and Beaton (1993). Subsequently, the Mdh genotypes of the 28 animals chosen as breeders (i.e., 7 males and 7 females of each homozygous genotype) were reconfirmed using a fresh tissue sample from each individual.

On 7 January 2000, we introduced each homozygous breeding family into a separate 1,000-l polyethylene cattle tank with 1 kg of waterlogged leaf litter. We observed embryos in the breeding tanks on 9 January, and on 12 January we removed approximately 500 embryos from each tank. Roughly half of the embryos from each family were stored at 25°C until hatching, while the other half was stored in a cold room (12°C and eventually down to 4°C) to retard embryonic development. The former embryos began hatching on or about 25 January (hereafter referred to as the “early” group), and the latter embryos (hereafter the “late” group) began hatching on 11 March, approximately 6 weeks after the rest of their cohort.

We reared larvae in 1,000-l high-density polyethylene cattle tanks filled to a depth of approximately 35 cm and containing 1.5 kg homogenized leaf-litter substrate. To minimize spatial difference among experimental units, we arranged the tanks in a 5 \times 6 grid (with two additional tanks appended to two of the rows) with approximately 0.5 m between neighboring tanks. The tanks were equipped with internal standpipes to hold the maximum depth constant. Water levels fluctuated below maximum according to evaporation and rainfall, but not significantly so. Each tank was inoculated repeatedly (about every 3 days) between 12 January and 10 March with a concentrated zooplankton mixture taken from a nearby ephemeral wetland, and the tanks were left uncovered to encourage oviposition by insects. Early hatchlings were added to tanks on 2 February, and late hatchlings were added on 15 March, a difference in effective hatching date of 41 days. The densities we used (approximately 6 hatchlings/m² at low density and 12 hatchlings/m²) were within the range observed among natural populations in this area (0.7–30.0 larvae/m²; Semlitsch 1987a), and are comparable to those used in other *A. talpoideum* mesocosm experiments (e.g., Semlitsch and Gibbons 1985; Semlitsch 1987a, b; Semlitsch and Reichling 1989; Ryan and Semlitsch 1998). Beginning in June, we searched the ponds visually every other night for metamorphic individuals, collecting them by hand using an aquarium net. We also placed plastic minnow traps in the tanks as a passive means of capturing metamorphs; gilled individuals were released from the traps each morning. The first metamorph was collected on 8 June and the last on 30 June.

About 270 days after the start of the experiment (on 26–27 October 2000), we drained the tanks and searched by hand through the leaf litter to recover all surviving individuals. We took a tissue sample (tail tip) from each individual for genotype determination before sacrificing by freezing. Each carcass was later fixed in 10% formalin. Following fixation, we dissected each individual (n=344) to assess reproductive condition, as determined by gross inspection of gonads. Each individual was assigned a maturation score ranging from one (immature) to four (mature and in breeding condition; for details see Ryan and Semlitsch 1998; Winne and Ryan 2001). To guard against bias in scoring reproductive condition, all determinations were made blindly with regard

to family identity or timing of hatching. Each individual was also measured for snout-vent length (SLV in millimeters; the distance between the tip of the snout and the posterior margin of the cloacal aperture).

We were interested in the effect of time of hatching on basic fitness components: survival, growth, and maturation. To determine the effect on overall survival, we used three-way analysis of variance (ANOVA) to analyze the differences between the eight treatments. Density (low or high), timing of addition of family A (early or late), and timing of addition of family B (early or late) were all main effects, with the angular-transformed proportion of individuals surviving to the end of the experiment as the response variable. We could not evaluate the survival of each genotype separately using ANOVA models because empty cells were prevalent in some treatments (i.e., survival was frequently zero for one family or the other in asynchronous treatments). Therefore, we used goodness-of-fit tests to determine whether the genotypes of survivors were significantly skewed from parity within each treatment combination. We also used a three-way ANOVA to assess size differences of surviving branchiates among the treatments, with log-transformed SVL as the response variable. Preliminary analyses indicated that SVL was negatively correlated with the number of survivors within treatments, so we used the angular-transformed proportion of survivors as a covariate.

Many of the mesocosms contained no immature gilled individuals, thus precluding the use of parametric statistics to analyze the effect of asynchronous hatching on maturation. We calculated the average maturation score for each treatment combination, ranked these values, and used Friedman's rank test to look separately at the effects of density (with the timing of addition combination as a blocking factor) and timing of addition (with density as a blocking factor). Relatively few animals completed metamorphosis in our experiment, necessitating the use of separate t-tests for size and age at metamorphosis, and goodness-of-fit tests to determine differences in the number of metamorphs with regard to density and hatching synchrony.

Results

Survivorship varied widely across the experiment [Fig. 1, experiment wide mean (SE): 0.42 (0.064)] although it did not differ across treatment combinations [Density: $F_{1,23}=0.69$, $P=0.414$; Addition of family A: $F_{1,23}=0.96$, $P=0.337$; Addition of family B: $F_{1,23}=1.28$, $P=0.269$; none of the interactions among main effects were significant (all $P>0.1$)]. When hatchlings were added synchronously, regardless of the density, individuals of both families survived to the end of the experiment with equal likelihood (Fig. 2). However, in each case where hatchlings were added asynchronously, the survivorship of individuals added later was significantly reduced ($P<0.0001$) and effectively zero (Fig. 2).

Fig. 1

The correlation between body size and survivorship among aquatic individuals (reproductive status undetermined). Circles (filled denotes low density; unfilled denotes high density) represent replicate mesocosms; symbols with error bars (± 1 SE) represent density means

Fig. 2

Family-specific survivorship in low- and high-density ponds. Bars (unfilled family A; filled family B) represent treatment means (+1 SE). χ^2 values are from goodness-of-fit tests for differences between families within each treatment combination; asterisks indicate a significant effect at $P < 0.0001$

At the end of the experiment, gilled individuals in the low-density mesocosms were significantly larger than those reared under high-density conditions ($F_{1, 22} = 18.00$, $P < 0.0001$), even after removing the strong effect of survivorship on size ($F_{1, 22} = 75.91$, $P < 0.0001$; Fig. 1). The timing of each family's addition had no effect on size (Addition of family A: $F_{1, 22} = 1.00$, $P = 0.329$; Addition of family B: $F_{1, 22} = 0.28$, $P = 0.602$) nor did any of the interactions (all $P > 0.1$), indicating that late hatching larvae obtained the same size of early hatching larvae in treatments where they survived to the end of the experiment. Maturation of aquatic adults was influenced by density (Friedman's $S = 4.00$, $df = 1$, $P = 0.046$) with low-density replicates having fewer immature individuals at the end of the experiment (Fig. 3). However, individuals did not exhibit differential maturation between synchronous and asynchronous treatments ($S = 6.00$, $df = 3$, $P = 0.112$). The absence of timing of addition effects in the synchronous treatments (i.e., both families early or both families late) indicates that our manipulations of incubation time did not adversely affect growth, development, or survival.

Fig. 3

Proportion of survivors remaining immature across treatment combinations

Only 10 of the 344 survivors in the experiment completed metamorphosis (3%) and these individuals came from only 6 of the 32 mesocosms (19%). The low rate of metamorphosis is not uncommon from a population like Dry Bay where gilled adults are more common than terrestrial adults (see Semlitsch and Gibbons 1985; Semlitsch et al. 1990). All ten metamorphs appeared in a 22-days time span (8–30 June) regardless of whether they were representative of early (60% of metamorphs) or late (40%) additions. Thus, while the date of metamorphosis was fairly restricted, there was appreciable difference in the ages at metamorphosis between larvae that hatched at different times [mean days to metamorphosis (± 1 SE): early-hatching = 135.0 (3.17), late-hatching = 92 (0); $t_{5, 0.05} = 13.55$, $P < 0.0001$]. The difference in size at metamorphosis was negligible [mean SVL (mm) at metamorphosis (± 1 SE): early-hatching = 46.0 (1.75), late-hatching = 43.3 (0.63); $t_{5, 0.05} = 1.23$, $P = 0.123$]. Most of the metamorphs (80%) came from high-density tanks ($\chi^2 = 3.6$, $df = 1$, $P = 0.0578$), but came from synchronous and asynchronous treatments with equal frequency ($\chi^2 = 0.4$, $df = 1$, $P = 0.527$).

Discussion

Our goal was to estimate the fitness effects of breeding and hatching asynchrony exhibited by aquatic and terrestrial adult morphs of *A. talpoideum*. The early and late hatchlings in this experiment simulate the offspring of aquatic and terrestrial parents, respectively, breeding asynchronously in the same pond. We found that the early versus late hatching alone does not influence body size, maturation, the likelihood of metamorphosis, or the size at metamorphosis, but asynchronous hatching has a profound negative effect on the later-hatching members of the population; specifically, only 2 of the 16 asynchronous mesocosms contained survivors from later-hatching families, and they constituted a clear minority (1 or 2 individuals) in those mesocosms. Thus, intraspecific priority effects in *A. talpoideum* may be important in regulating populations in

much the same way as interspecific priority effects can be, with early-hatching *A. opacum* decreasing survival of later-hatching *A. talpoideum* (Boone et al. 2002).

Decreased survival of late-hatchers may have been due to malnutrition (via competitive inferiority with larger early-hatchers) or cannibalism. Intraspecific aggression and cannibalism are common in *A. talpoideum* (Semlitsch 1987a; Semlitsch and Reichling 1989) and cannibalism in particular is more likely when a significant size asymmetry exists among members of the population (Collins and Holomuzki 1984; T.J. Ryan, personal observation). We did not measure the degree of size asymmetry between early- and late-hatching larvae at the time of introduction. In laboratory experiments where individual growth rate was controlled (by resource availability) and measured, larval *A. talpoideum* were 3 times larger than hatchlings (measured in terms of SVL) at 40 days post-hatching (Ryan and Semlitsch 2003; T.J. Ryan, unpublished data), indicating the potential—if not the likelihood—for a significant size asymmetry between early- and late-hatchers in the current experiment. Likewise, we did not directly measure resource levels in the mesocosms prior to or following the late addition, and thus we cannot definitively identify resource limitation as a source of reduced survival in our experiment. However, previous long-term field studies (Semlitsch et al. 1996) indicated that interspecific competition is a strong regulatory factor, a finding backed up by controlled mesocosm experiments (Semlitsch 1987a, b; Ryan and Semlitsch 1998). The results of our experiment demonstrate that aquatic adults may have a significant fitness advantage over terrestrial adults through enhanced survival of offspring when the breeding of adult morphs is asynchronous, regardless of the exact cause.

The presence of intraspecific priority effects in polymorphic *A. talpoideum* populations may provide important insight into the evolution and ecology of alternative life-cycles. Moran (1994) defined complex life-cycles (hereafter CLC) as having at least two discrete post-embryological morphologies, usually with associated discrete ecologies, as is common in the Amphibia. Salamanders that bypass metamorphosis in favor of an aquatic adulthood thus demonstrate a simple life-cycle (hereafter, SLC). Whiteman (1994) proposed that relative fitness advantages are a key to understanding the differential expression of CLCs and SLCs in polymorphic salamanders. In Whiteman's model, fitness differences between metamorphic and aquatic adults (and thus the CLC and SLC, respectively) are explicitly due to differences in body size (see Figs. 1 and 2, Whiteman 1994). This model builds directly from the predictions of the Wilbur and Collins (1973) optimality model of amphibian metamorphosis, which predicts that metamorphosis should be delayed as long as larval growth is increasing or remaining consistently high, with metamorphosis occurring only once a maximal size threshold is broached. For salamander species that bypass metamorphosis, the SLC is predicted when growth opportunities are good and aquatic adults can achieve a large body size, which is equated with high fitness, relative to the smaller members of the population that undergo metamorphosis and complete the CLC. This is called the "Paedomorph Advantage" hypothesis by Whiteman, and is contrasted with an alternative, the "Best-of-a-Bad Lot hypothesis", which casts the SLC as a concession or compromise, a way of salvaging some fitness through reproduction as an aquatic adult when metamorphosis (and thus the CLC) is a better but unavailable option. According to the Best-of-a-Bad Lot hypothesis, metamorphic adults are larger than aquatic adults because metamorphic failure is a result of poor larval growth. For both

hypotheses in Whiteman's model, larval growth determines adult body size, and adult body size in turn determines fitness and the prevalence of the alternative life-cycles.

Ryan and Semlitsch (2003) tested the hypothesized link between larval growth rate and life-cycle expression, finding that relatively low growth and relatively robust growth, especially later in larval development, were significantly associated with the aquatic and terrestrial adults, respectively. This result supports the expectations of the Best-of-a-Bad Lot hypothesis. Also supporting the hypothesis is the fact that clutch size is positively correlated with body size in female *A. talpoideum* (as it is with most amphibians) and metamorphic females are larger and produce correspondingly larger clutches than same-age aquatic females (Semlitsch 1985). According to Whiteman's model, when metamorphic adults are larger than aquatic adults, the latter occur primarily in unfavorable aquatic habitats that feature high intraspecific competition, predation and poor growing conditions because of low food supplies, low temperatures, or short growing seasons. However, several experiments have found lower frequency of aquatic adults (or conversely, higher frequency of metamorphosis) under the ecological conditions predicted to be associated with the Best-of-a-Bad Lot hypothesis, such as high density (Semlitsch 1987*a, b*; this study) and high predation (Jackson and Semlitsch 1993). Furthermore, the expected ties between larval growth rate, adult body size, and fitness predicted by the Whiteman model are complicated by the findings that precocious maturation (Ryan and Semlitsch 1998) and early reproduction (Scott 1993; Krenz and Sever 1995) may lead to higher reproductive success (this study) that offsets or compensates for any size-based fitness effects.

The importance of fitness differences between aquatic and metamorphic adults and the source of such differences are important for understanding evolution and maintenance of life-cycle polymorphisms, as considered by Whiteman (1994). However, the relationship between proximate mechanisms (e.g., larval growth and physiological processes), fitness determinants (e.g., adult body size and the timing of reproduction), and environmental conditions (e.g., larval density, predation risk, long-term hydroperiod cycles) is not straightforward—and does not necessarily conform to either of the Paedomorph Advantage or Best-of-a-Bad Lot hypotheses in Whiteman's model—in the model organism, *A. talpoideum*. Our results suggest that body size should not be assumed to be the primary fitness determinant in polymorphic salamanders; a reliance on the Wilbur and Collins (1973) optimality model leads to such an assumption. Models of metamorphic timing that consider the relative costs and benefits of aquatic versus terrestrial survival (Werner 1986) and developmental flexibility (Leips and Travis 1994) may be informative to understanding the ecology and evolution of polymorphic life-cycles given that a complex and diverse set of factors, many of which are independent of body size, are important in life-cycle expression; e.g., courtship patterns (Denoël et al. 2001), sex-specific payoffs (Whiteman 1997; Winne and Ryan 2001), physiology (Ryan and Hopkins 2000; Boorse and Denver 2002; Currens et al. 2002), genetic factors (Semlitsch et al 1990; Voss et al. 2003), and spatio-temporal variation in habitat quality (Ryan and Semlitsch 2003).

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