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Aspects of Sex-Specific Differences in the Expression of an Alternative Life Cycle in the Salamander *Ambystoma talpoideum*

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A recent evolutionary ecological model of facultative paedomorphosis predicts that body size of mature individuals should be larger than immatures of the same cohort. We investigated sex-specific differences in body size and maturation within a single cohort of branchiate (= larval and paedomorphic) mole salamanders, *Ambystoma talpoideum*. In addition, we also sampled the population after the breeding season, as some individuals began to undergo metamorphosis and leave the pond. The branchiate population was female-biased (62.7%), and mature (paedomorphic) females were significantly smaller than paedomorphic males or immature (larval) females. The majority of male branchiates were mature (86.6%), whereas significantly fewer females were mature (64.4%). After the reproductive season, males and females underwent metamorphosis in the same proportion in which they occurred in the branchiate population, although a significantly greater proportion of immature females metamorphosed (64.6%) compared to their frequency in the branchiate population (35.6%). There were no significant differences in body size with regard to sex or maturation among metamorphosing individuals. Our data demonstrate that maturation in branchiates is independent of body size in males and that it may negatively affect body size in females. Our findings underscore sex as a potentially important factor, and question the role of body size, in regulating this life cycle polymorphism in *A. talpoideum*.

THE aquatic habitats used by amphibians as nuptial/natal sites are often temporally and spatially variable and frequently fluctuate widely in quality and quantity within a relatively short span of time (Semlitsch et. al., 1996). Amphibians have evolved a diverse array of adaptations that allow for the continued use of aquatic habitats with varying conditions. Both rapid (Newman, 1989) and delayed (Bruce, 1980) metamorphosis have been regarded as adaptations to local environmental regimes, as have other biological innovations, such as facultative cannibalism (Collins and Cheek, 1983; Pfennig, 1990) and varied egg-laying strategies (Duellman, 1988).

Most temperate-zone amphibians exhibit a complex life cycle, where metamorphosis from an aquatic, larval stage into a terrestrial form precedes maturation and reproduction. However, there are departures from the general complex life cycles pattern in many salamander families. Some species demonstrate a life cycle polymorphism in which rather than undergoing metamorphosis prior to maturation, individuals may become sexually mature while bypassing morphological metamorphosis altogether. This life cycle polymorphism is known as facultative paedomorphosis [Semlitsch, 1985; Harris, 1987; Whiteman, 1994; also referred to as paedogenesis (Reilly et al., 1997)]. Facultative paedomorphosis may be an adaptation to, and maintained by, fluctuating environmental conditions that promote varying selective pressures (Harris, 1987). The ability to undergo different developmental pathways may allow species with this polymorphism to capitalize on differential growth opportunities in aquatic and terrestrial environments (Wilbur and Collins, 1973; Semlitsch et. al., 1990; Whiteman, 1997).

The mole salamander, *Ambystoma talpoideum*, has been an important model organism for understanding the evolution and ecology of the life cycle polymorphism. In *A. talpoideum*, individuals are immature immediately following metamorphosis (Jackson and Semlitsch 1993; Ryan and Semlitsch, 1998; Ryan, 2000) and require several months (or longer) in the terrestrial environment to achieve maturation (Semlitsch et al., 1988). Nonmetamorphosing individuals may remain immature, overwinter, and metamorphose in the following year or become mature branchiates (= paedomorphs). Experimental manipulations of critical ecological factors have been important in making comparisons of individuals of known age and parentage expressing alternative life cycles in *A. talpoideum* (e.g., Semlitsch and Gibbons, 1985; Semlitsch, 1987; Ryan and Semlitsch 1998). It has been much more difficult to monitor the patterns of expression in natural populations in any comprehensive manner, primarily because of large population sizes and wide overlap in body size and appearance of individuals belonging to different cohorts. Occasionally, however, natural disturbances create a situation where we may be able to study aspects of life cycle expression in natural settings with a high degree of confidence in the parentage and age of individuals. For example, after pond drying resulted in the loss of the paedomorphic portion of a population, Semlitsch (1985) was able to study reproductive aspects of metamorphic and paedomorphic *A. talpoideum* as the paedomorphic population was reestablished in following year(s). Scott (1993) investigated aspects of reproductive ecology of *A. talpoideum* when a (usually) temporary pond held water continually for more than a year, allowing for the expression of the paedomorphic phenotype in a normally metamorphic population.

Following a hydrological anomaly (i.e., an extremely wet year), we studied the first generation of branchiate (= both mature and immature nonmetamorphic individuals) *A. talpoideum* in a natural population. Thus, we were able to look at the expression of an alternative life cycle in a single cohort without the confounding effects of other cohorts. Because there are no reliable field data on sex ratios or the effects of sex on other traits (e.g., body size) in natural populations of paedomorphic *A. talpoideum*, we focused our attention on these characteristics in this paper. We compared size of immature larvae (those neither metamorphosing nor maturing the first year) to that of paedomorphic individuals in the context of a model of facultative paedomorphosis (Whiteman, 1994). Furthermore, we examined sex-specific differences in size and expression of maturation among branchiates and the frequency of metamorphosis of branchiates among the sexes and reproductive classes following the completion of the first reproductive season.

MATERIALS AND METHODS

Collection site.—We collected *A. talpoideum* from Carolyn's Bay, a 0.5-ha Carolina bay located on the U.S. Department of Energy's Savannah River Site in Aiken County, South Carolina. Carolina bays are shallow, elliptical depressions found throughout the Atlantic Coastal Plain of the southeastern United States (R. R. Sharitz and J. W. Gibbons, USFWS, 1982, unpubl.) that serve as major breeding sites for many species of amphibians (Gibbons and Semlitsch, 1991). In most years, Carolyn's Bay is a temporary wetland, filling via rainfall in late autumn or early winter and drying during the summer (R. Semlitsch, pers. comm.). The period of pond filling roughly corresponds to the breeding season of *A. talpoideum* (Semlitsch et al., 1993). Occasionally, however, Carolyn's Bay does not dry completely; the bay filled in the fall of 1997 and continued to hold water throughout 1998 (R. Lide, unpubl. data). Any branchiate animals collected in the bay during the course of our sampling (see below) could be unambiguously identified as members of the 1997–1998 hatchling cohort. Members of the next cohort (i.e., 1998–1999) would have had to grow at rates four times greater than that expressed by the 1997–1998 cohort to reach the body sizes we report here. Furthermore, the presence of a full (or nearly full) compliment of mature ovarian follicles in many females in our sample indicates that the breeding activity that would have produced the 1999–2000 cohort had not been completed by the time of our sampling.

Collection methods.—We collected branchiate salamanders using unbaited minnow traps. Fifty metal stakes that had been systematically placed in a grid throughout the bay prior to this study were used as trap sites. To reduce bias in the placement of traps, we randomly selected 10 trap sites without replacement for each of the five sampling nights: 28 and 31 January, 4, 7, and 10 February 1999. On the morning of each of the sampling nights, minnow traps were set and fastened to the appropriate stake. On the following mornings, all *A. talpoideum* were collected from the minnow traps, and the depth of each trap was recorded to the nearest 0.5 cm. The branchiate salamanders ($n = 260$) were then transported to the lab, sacrificed in a dilute solution of chloretone, and immediately preserved in a solution of 10% neutral buffered formalin.

In January 1999, we erected a partial drift fence to encircle approximately 70% of the circumference of the bay. The drift fence was constructed in five sections varying from 30–100 m in length and made of high-grade erosion cloth, which was buried 5 cm below the surface to prevent salamanders from passing under the fence. We placed 20-L pitfall traps every 10 m along the fence. All fence sections were located approximately 20 m from the water's edge at the time of construction. On 25 March 1999, during a mass emigration from the bay, we collected recently metamorphosed individuals (as evidenced by the incomplete resorption of the gills) at a haphazardly selected section of the fence. These specimens ($n = 139$) were transported to the laboratory where they were sacrificed and preserved as described above.

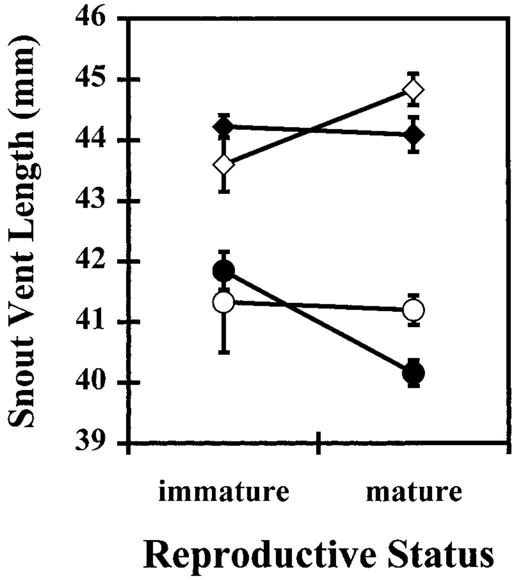

Fig. 1. Mean (± 1 SE) size of mature and immature *Ambystoma talpoideum* from Carolyn's Bay. Branchiates, collected in the bay during late January to early February, are represented by circles; recent metamorphs, collected at the drift fence in late March, are represented by diamonds. In each collection, closed symbols are used for females and open symbols are used for males.

TABLE 1. SEX AND MATURATION STATUS OF *Ambystoma talpoideum* FROM TWO COLLECTIONS AT CAROLYN'S BAY. The raw number (and proportion) of each sex in collection is reported; the number (and proportion) within each combination of phenotype and sex is also reported. The collection of branchiates was made in late January to early February; the collection of metamorphs was made in late March (see text for details).

Collection	Female	Male
Branchiate, $n = 260$	163 (0.627)	97 (0.373)
mature	105 (0.644)	84 (0.866)
immature	58 (0.356)	13 (0.134)
Metamorphosed, $n = 139$	96 (0.691)	43 (0.309)
mature	34 (0.354)	36 (0.837)
immature	62 (0.646)	7 (0.163)

Dissections.—We recorded the snout–vent length (SVL, length from the tip of the snout to the posterior margin of the vent, ± 0.5 mm) of each individual, then dissected each to determine sex and reproductive status. Mature females were characterized by the presence of enlarged yolky ovarian follicles and/or enlarged, convoluted oviducts. Mature males were identified by the presence of enlarged testes and/or highly coiled vasa deferentia (Semlitsch, 1985). We regarded all individuals that exhibited both the larval morphology (external gills and extensive tail fins) and sexual maturity as paedomorphs. All other branchiates were regarded as immature larvae. The same criteria of maturation apply to metamorphosing individuals (i.e., those caught emigrating from the bay); all immature metamorphs were comparable to immature larvae, whereas all sexually mature metamorphs had previously reproduced (or at least had the option to reproduce) as paedomorphs.

Analysis.—We expected the mean size of metamorphs to be larger than branchiates, as the former were collected 1.5–2 months later than the latter and, thus, had additional time for growth. This size difference was confirmed upon preliminary analyses [analysis of variance (ANOVA) of SVL: $F_{1,398} = 220.9$, $P < 0.0001$ (all body sizes were log-transformed to meet the assumptions of parametric tests); Fig. 1]. Therefore, we tested for size differences resulting from sex and reproductive status within both the branchiate and metamorphic collections using single factor ANOVAs of SVL.

We calculated the proportions of mature and immature individuals of each sex in each collection. For the branchiate collection, we used goodness-of-fit tests to detect deviations from parity between sexes and to examine differences in the expression of maturation within each sex. We used the same tests to look at differences in the metamorph collection; however, in these tests, we used the proportion of each sex/maturation combination in the branchiate collection as expected values.

RESULTS

Branchiates.—The sex ratio of our collection (mature and immature combined) was significantly female biased (Table 1; $\chi^2 = 16.7538$, df $= 1$, $P < 0.0001$). A goodness-of-fit test demonstrated that maturation was not independent of sex, with more mature males and more immature females than expected ($G = 16.2294$, df $= 3$, $P < 0.005$). Both immature females and mature males were significantly larger than paedomorphic females (Fig. 1; immature females: $F_{1,161} = 20.65$, $P < 0.0001$; mature males: $F_{1,187} = 10.48$, $P = 0.0014$). There were no significant differences in size between the immatures of the sexes ($P = 0.4803$) or between paedomorphic and immature males ($P = 0.8978$).

Metamorphs.—The pattern of sex- and maturity-based size differences among metamorphs was different than in the branchiates (Fig. 1). Immature metamorphs were of the same size, regardless of sex ($P = 0.2923$). There was no significant difference in size between the mature and immature females ($P = 0.6695$). Mature males tended to be larger than immature males ($F_{1,42} = 4.00$, $P = 0.052$), and mature males were larger than mature females ($F_{1,69} = 3.84$, $P = 0.0542$), although these differences were only marginally significant.

With regard to sex, metamorphs left the bay in the same proportions as were present in the branchiate collections (Table 1; $\chi^2 = 2.4133$, df $= 1$, $P = 0.1203$). However, there was a significant change in the proportions of mature and immature females at metamorphosis when compared to their representation in the population as branchiates 1.5–2.0 months earlier ($G = 33.6671$, df $= 3$, $P < 0.0001$); mature females were far more numerous in the branchiate class compared to the metamorphic class (Table 1).

DISCUSSION

We found the branchiates from the 1997–1998 cohort at Carolyn's Bay to be significantly female biased. Because we did not encircle the bay with the drift fence prior to the emigration of the earliest metamorphs from the cohort (i.e., those that metamorphosed prior to maturation as in most other amphibians), we cannot be certain whether the observed trend is representative of a populationwide female bias or a greater propensity of males to initiate prematuration metamorphosis. Likewise, we cannot rule out differential mortality of the sexes as a contributing factor to this bias. A paucity of data exists regarding morph-specific sex ratios in natural populations of facultatively paedomorphic salamanders; in summarizing the available data, Whiteman (1997) found that, when sex ratios deviated from parity in paedomorphic salamander populations, they were most often female biased, as in the present case. Ours, however, are the first data from a natural population of *A. talpoideum*.

Whiteman's (1994) model of facultative paedomorphosis places emphasis on the role of body size in determining the relative fitness of metamorphs, paedomorphs, and immature larvae. Among the assumptions of the model is that larval growth rate is an important component of adult body size and thus plays a significant role in determining the expression of alternative life cycles. In our study, we found no appreciable difference in the size of immature and mature male branchiates of the same cohort, and immature female larvae were found to be significantly larger than their mature counterparts. Therefore, our findings may be regarded as conditional support for Whiteman's (1994) Best-of-a-Bad Lot (BOBL) hypothesis. This hypothesis suggests that paedomorphosis results from relatively slow growth rates and, therefore, small adult body size. It appears that relatively slow growth rates led to paedomorphosis in female *A. talpoideum*. Unfortunately, we cannot compare the sizes of the paedomorphic females with metamorphic females, because the latter portion of the population was not monitored. The absence of a difference in body size among immature and mature branchiate males and the fact that immature branchiate females were larger than the matures is consistent with neither the BOBL hypothesis nor the alternative hypotheses of Whiteman's model.

As mentioned above, the relative fitness of the morphs is determined predominantly by body size in Whiteman's (1994) model of facultative paedomorphosis. The model predicts that immature individuals are always less fit and should always be smaller than matures, be they metamorphic or paedomorphic (see table 1, fig. 2 in Whiteman, 1994). Several studies have failed to detect differences in body size among metamorphs, paedomorphs, and immature larvae of a single cohort (e.g., Licht, 1992; Jackson and Semlitsch, 1993; Ryan and Semlitsch, 1998). Furthermore, in laboratory studies, differences in larval growth rates do not necessarily result in the differential expression of metamorphosis and maturation. Ryan (2000) found a complex relationship between larval growth rates and life cycle expression in *A. talpoideum*, such that the overall growth rate is far less important than a particular point during larval development at which different growth rates are experienced. No clear connection between larval growth rate, body size, and metamorphosis/paedomorphosis was found in a laboratory experiment using *A. tigrinum* (S. R. Voss, unpubl. data). Thus, larval growth rate and body size may not be closely tied to the expression of alternative life cycles, or perhaps such a relationship is context- or species-specific.

One explanation for the difference in body size among branchiate females is grounded in reproductive investment theory (Trivers, 1972). Maturing females invest significant energy in reproductive development that may come at a cost to somatic growth. Because immature females make no investment in reproduction, all available energy (aside from that required for maintenance and metabolism) goes toward somatic growth or fat storage. In other words, immature females can continue growing while the maturing individuals direct their energy into costly ova production, possibly sacrificing somatic growth. In our study, there was no difference in the sizes of immature and mature male branchiates. Theory supports this result as well, because the energy necessary for a male to mature is minimal and relatively inexpensive. Differences in reproductive investment between the sexes can also account for why we found mature males to be larger than females. For example, Ryan and Hopkins (2000) determined that large paedomorphic females have considerably higher standard metabolic rates (and thus less energy available for growth) than similar-sized males.

The high cost of egg production in females may result in a trade-off in current versus future reproduction (Stearns, 1992; Roff, 1992; Scott and Fore, 1995). Females remaining immature throughout the first year may offset any immediate losses in fitness by achieving a larger body size at the time of future reproductive events (perhaps consistent with some predictions of the BOBL hypothesis). This is especially relevant in female *A. talpoideum* and similar animals whose fecundity is closely correlated with body size (Salthe, 1969; Kaplan and Salthe, 1979; Semlitsch, 1985).

Data on the frequency of metamorphosis following one or more years of paedomorphic breeding in species with flexible life cycles, as typified by *A. talpoideum*, are few. The lack of reliable data has led to wide speculation on how often postreproduction metamorphosis occurs (e.g., Reilly et al., 1997). In our study, there appeared to be no sex bias in postreproduction metamorphosis; males and females left the bay in the same proportions in which they were documented 1.5–2.0 months earlier. Patterns of metamorphosis within each sex, however, were different. The ratio of immature to mature metamorphic males in March was the same as the ratio of immature and mature branchiate males in January. Mature females were less likely to undergo metamorphosis when compared to immature larval females. We suggest that the phenology of *A. talpoideum* may explain why paedomorphic females were less likely to undergo postreproduction metamorphosis.

The migration of metamorphic adults to the breeding site is constrained by climatic factors, primarily rainfall and temperature (Semlitsch, 1985; Semlitsch and Ryan, 1998). Paedomorphic adults, however, may initiate (and in some cases complete) courtship, insemination, and oviposition prior to the arrival of metamorphic adults, thereby providing their offspring a potentially large head start in larval development and, thus, a competitive advantage over the offspring of metamorphs (Scott, 1993; Krenz and Sever, 1995; Ryan and Semlitsch, 1998). Although both sexes are likely to incur a cost of metamorphosis as a result of climatological restriction of breeding opportunities, males are influenced less than females, because the former arrive earlier and may initiate courtship with already present paedomorphic females (Semlitsch at al., 1993; Semlitsch and Ryan, 1998). A model incorporating aquatic versus terrestrial growth opportunities and associated gains in fecundity along with habitat-specific mortality schedules (Werner, 1986) would be appropriate in this regard but is beyond the scope of the data collected in our study.

We took advantage of a rare occurrence, the production of a paedomorphic class of salamanders in a normally metamorphic population, to examine poorly understood aspects of a life cycle polymorphism in *A. talpoideum*. Our findings imply that models and hypotheses that fail to take sex-specific differences into account may be too simple because selection may, and often does, operate differently on different sexes (Andersson 1994), just as it does on different morphs (Roff, 1996). Following Whiteman (1997), we recommend that sex-specific attributes of organisms be considered when testing or developing hypotheses for alternative life cycles.

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