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TIME AND SIZE AT METAMORPHOSIS RELATED TO ADULT FITNESS IN *AMBYSTOMA TALPOIDEUM*[1]

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Abstract. The relationships among timing of metamorphosis, size at metamorphosis, and traits related to adult fitness were studied for 8 yr in the salamander *Ambystoma talpoideum* at a temporary pond. Among years, the modal time of metamorphosis and mean body size at metamorphosis were positively correlated with the date the pond dried. In years that the pond dried late, one group of larvae metamorphosed well before the pond dried, whereas the other group metamorphosed just before pond drying. Mean body size of late-metamorphosing individuals was not greater than that of individuals metamorphosing early. Early-metamorphosing males and females were larger at first and second reproduction than were late-metamorphosing individuals.

Independent of timing of metamorphosis, larger juveniles at metamorphosis were also larger adults at first reproduction. Age at first reproduction for males was not associated with timing of or size at metamorphosis but large early-metamorphosing females reproduced at a younger age than did small early-metamorphosing females. Neither time of metamorphosis nor size at metamorphosis was associated with survival to first reproduction.

These results demonstrate a direct relationship between phenotypic variation generated in the larval stage and adult traits closely associated with an individual's fitness.

Key words: Ambystoma talpoideum; *amphibian; body size; fitness; growth; metamorphosis; population dynamics; reproduction; salamander; survival; temporary pond.*

INTRODUCTION

Metamorphosis defines the transition from the larval stage to the adult stage of species with complex life cycles such as insects, parasites, and amphibians. The transition often is from a period of relatively fast growth as a larva to a period of reproduction and dispersal as an adult. Variation among individuals and populations in the timing of metamorphosis is widespread (Gilbert and Frieden 1981), especially in amphibians (Wilbur and Collins 1973, Wilbur 1980). The optimal timing of metamorphosis involves compromises between growth, development, and survival of the larva and growth, reproduction, and survival of the adult (Istock 1967, Wilbur 1980, Policansky 1983, Stearns and Koella 1986, Werner 1986). The timing of metamorphosis can influence associated traits such as body size at metamorphosis that potentially may affect adult survival, body size at first reproduction, age at first reproduction, and fecundity (Moeur and Istock 1980, Prout and McChesney 1985).

Amphibians can metamorphose after a minimum larval period set by a minimum body size but often remain longer in the larval stage (Wilbur and Collins 1973, Alford and Harris 1987). When resources are in short supply, metamorphosis can be delayed by the slower growing individuals to increase their body size at metamorphosis or simply to attain the minimum body size to initiate metamorphosis (Semlitsch and Caldwell 1982, Travis 1984). In a productive habitat or with high per capita resources, however, individuals may vary little in body size at metamorphosis or length of the larval period (Collins 1979, Travis 1984). Abundant resources may also generate a positive relationship between body size and larval period if fast-growing larvae metamorphose early, lowering effective density and leaving higher per capita resources to the remaining, slow-growing larvae. Under conditions of high but declining resources, populations of larvae may generate a negative relationship between body size at metamorphosis and larval period (Alford and Harris 1987). In general, amphibian larvae appear to respond to an enhanced food supply by delaying metamorphosis until a maximum size is reached and to respond to a decreased food supply by initiating metamorphosis (Alford and Harris 1987).

Although much is known about variation in growth, development, and timing of metamorphosis for larval amphibians under experimental laboratory conditions (Wilbur and Collins 1973, Smith-Gill and Berven 1979,

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Wilbur 1980, Alford and Harris 1987), little is known about variation in these traits in natural populations (Wilbur 1972, Collins 1979, Berven and Gill 1983, Smith 1983). Even less is known concerning how variation in larval traits affects postmetamorphic growth, survival, and reproductive performance (Semlitsch 1987*c*).

Large body size at metamorphosis may result in large size at first reproduction in amphibians. This intuitive and frequently asserted relationship has been demonstrated only twice, in the frogs *Rana sylvatica* (Berven and Gill 1983) and *Pseudacris triseriata* (Smith 1987). Large body size and early metamorphosis are also correlated with early first reproduction in *P. triseriata,* but not with survival (Smith 1987). Similar relationships between any larval traits and factors associated with adult reproductive success have not been documented for any natural population of salamanders. Adult body size of amphibians is often related to mating success in males (Howard 1980, 1983, Berven 1981, Verrell 1982) or related to the number and size of eggs produced by females (Salthe 1969, Kaplan and Salthe 1979, Berven 1982, Semlitsch 1985*a*). Variation in age at first reproduction can affect the timing and amount of reproduction. In addition, age at first reproduction has theoretically been considered the most important trait influencing the intrinsic rate of increase in a population (Cole 1954, Lewontin 1965, Meats 1971, Bell 1976, 1980).

This study documents variation in timing of metamorphosis and size at metamorphosis in a natural population of the salamander *Ambystoma talpoideum* and tests the effects of these variables on adult body size, survival, and age at first reproduction. Since larval growth and survival were not measured or manipulated, theoretical models of the optimal timing of metamorphosis (Wilbur and Collins 1973, Stearns and Koella 1986, Werner 1986) could not be tested (see Alford and Harris 1987). Postmetamorphic demographic data such as we present, however, are a prerequisite for tests of these models.

We tested the following null hypotheses with our field data by comparing early and late or large and small metamorphosing larvae: (1) metamorphosing late does not affect body size at metamorphosis; (2) large body size at metamorphosis or early metamorphosis does not affect body size at first reproduction; (3) large body size at metamorphosis or early metamorphosis does not affect age at first reproduction; and (4) large body size at metamorphosis or early metamorphosis does not affect survival to first reproduction.

Natural history

Ambystoma talpoideum migrate to ponds from November through February in South Carolina, with oviposition occurring during a relatively short period (<30 d) in January or February (Semlitsch 1985*b*). Postbreeding adults emigrate primarily in March. Individuals move to surrounding terrestrial habitats where they remain in underground burrow systems until the next breeding season (Semlitsch 1981, 1985*b*). Individuals are usually philopatric to the pond from which they metamorphosed; some marked individuals returned to our study pond for >6 yr. Females oviposit 10–1000 eggs singly, scattering them across the pond bottom on leaves, grass, and twigs (Semlitsch 1985*a*). Eggs hatch in 30–40 d, and larvae are first found in the pond in late February or March. Larvae can begin metamorphosing in early May, but in some populations facultative paedomorphosis is common (Semlitsch 1985*a*).

METHODS

Study pond

The study was conducted for 8 yr at Rainbow Bay, Barnwell County, South Carolina, United States, on the United States Department of Energy's Savannah River Plant. The pond is a natural depression of unresolved geologic origin called a "Carolina bay" (Sharitz and Gibbons 1982). On the southeastern Atlantic Coastal Plain these freshwater bays are major breeding sites for many species of amphibians (Gibbons and Semlitsch 1982). During this study 27 species of amphibians were collected at Rainbow Bay. Rainbow Bay is ≈1 ha in area and has a maximum water depth of 1.04 m. It usually fills with water during winter and dries between April and September (Semlitsch 1985*a*). Rainbow Bay is surrounded by xeric habitats with deep, well-drained sandy soils. Description of the vegetation, drying cycle, rainfall, temperature, and other physical characteristics of the study site already have been reported (Semlitsch 1985*a, b,* 1987*a*).

Field sampling and marking techniques

A terrestrial drift fence constructed of 50 cm high aluminum flashing completely encircled Rainbow Bay (440 m in circumference). Paired pitfall traps (40-L buckets) were placed on opposite sides of the fence at 10-m intervals (see Gibbons and Semlitsch 1982). The flashing was buried in 10–15 cm of well-packed soil to prevent salamanders from crawling under the fence. Aluminum flashing has a relatively smooth surface and *A. talpoideum* have never been observed to climb over or crawl under the drift fences. Thus, a complete census of individuals migrating into and out of the breeding site was achieved each year, with a decreasing sampling error of 27–7% over time (see Gibbons and Semlitsch 1982: Table 5).

Pitfall traps at the drift fence were checked daily after installation on 21 September 1978 through 1 August 1986. In 1979, most metamorphosed juvenile *Ambystoma talpoideum* were individually marked by clipping toes in a unique combination. The remaining juveniles from 1979 and all juveniles produced in subsequent years (1980–1983 and 1985) were given "group" marks to distinguish annual cohorts. In 1984, juveniles that metamorphosed and migrated before 31 July were given a different group mark than those captured after that date. Thus, for both the 1979 and 1984 cohorts we could distinguish early metamorphs (i.e., individuals that emigrated while the pond still contained water, June–July) from late metamorphs (i.e., individuals that emigrated after or in response to the drying of the pond, August–October). Because oviposition and hatching of young occur each year during a relatively short time (<1 mo) the early groups were younger at metamorphosis than the late groups. We assumed that the timing of metamorphosis of larvae was positively correlated with the timing of juvenile emigration.

Regeneration of toes was greatest during the 1st yr of life, but since *A. talpoideum* can mature and breed in their 1st yr, many individuals were recaptured and toes were reclipped when necessary. The toe-clip of individuals with significant regeneration after 1–2 yr was still recognizable. Sex and female reproductive condition (gravid or nongravid: ova can be seen through the ventral surface of the abdomen) were recorded for adults returning to the breeding pond. Body size (snout–vent length, SVL) was measured to the nearest 0.5 mm from the snout to the posterior end of the cloaca for all individually marked juveniles and returning adults, and subsamples of group-marked juveniles. All salamanders were processed in the field and immediately released on the opposite side of the fence, the presumed direction of migration.

Statistical analyses

We tested for differences in size at metamorphosis, first among years and then between early- and late-metamorphosing groups within two years. The Kolmogorov-Smirnov D statistic to test for normality was computed for both the original body-size distributions and $\log_e$-transformed body-size distributions. The assumption of normality was not met for any of the distributions. However, due to the large sample sizes ($N > 44$) in each group, violation of the normality assumption should not seriously affect tests of differences among group means (Scheffé 1959). Therefore, we used parametric one-way analysis of variance and two-tailed t tests to compare among- and within-year differences in body size, respectively. Similarly, we used two-tailed t tests to examine group differences in adult size at first reproduction. Data were also tested for homogeneity of variances, and an approximate t test was performed if assumptions were violated (SAS 1982).

We used analysis of covariance to test the effects of size at metamorphosis and of time of metamorphosis (early vs. late) on size at first reproduction among the individually marked juveniles of the 1979 cohort. Size at metamorphosis was the covariate in a Type III sum of squares model (SAS 1982). Analysis of covariance was also used to test the effects of time and size at metamorphosis on age at first reproduction for metamorphosing juveniles from 1979. Because there was a significant interaction between size and time in this latter test for females, a linear regression analysis was performed between size at metamorphosis and age at first reproduction, separately for the early and late groups. Total survival for the 1979 cohort through 1984 was compared between early and late groups and among four size classes by G tests (log-likelihood ratio for a contingency table: Zar 1974). Data for males and females were analyzed separately when possible because of potential differences in the timing of maturity and reproduction between the sexes in amphibians (Berven and Gill 1983, Smith 1987).

The significance level was set a priori at $\alpha = .05$ for all statistical tests. All statistical analyses were performed using the Statistical Analysis System (SAS 1982).

RESULTS

Annual variation in metamorphosis

The timing of metamorphosis en masse varied among years in *A. talpoideum* at Rainbow Bay. Large numbers of metamorphosed juveniles were collected emigrating from the pond as early as May in 1982 and as late as October in 1984. The pond dried early in 1981, 1985, and 1986 (7 May 1981, 4 April 1985, and 24 April 1986) due to below-normal rainfall. No larvae metamorphosed from Rainbow Bay in 1985 or 1986, while only three larvae metamorphosed in 1981.

The modal date (day of the year) of metamorphosis was positively correlated with the date of pond drying (Spearman rank correlation: $r_s = 0.94$, $P = .0048$). Date of metamorphosis of the first individual, however, was not significantly correlated with the date of pond drying ($r_s = 0.54$, $P = .2657$).

The body size of metamorphosing larvae varied significantly among years ($F = 364.64$, df = 5,2243, $P < .0001$, $r^2 = 0.4489$; Fig. 1). The mean body size of metamorphs was positively correlated with the day of the year on which the pond dried ($r_s = 0.94$, $P = .005$; Fig. 2). Even without the potentially biased sample from 1981 ($N = 3$), the relationship was still significantly positive ($r_s = 0.90$, $P = .037$). Mean body size at metamorphosis was not correlated with any indirect estimate of larval density (total number of eggs, $r_s = 0.50$, $P = .263$; total number of metamorphosing juveniles, $r_s = 0.43$, $P = .289$; Semlitsch 1987*a*). A Tukey's studentized range test indicated that metamorphs were significantly larger in 1979 ($\bar{X} = 49.8$ mm SVL) and 1984 ($\bar{X} = 49.1$ mm SVL) when the pond dried on days 205 and 270, respectively, than metamorphs in 1980 ($\bar{X} = 43.5$ mm SVL) and 1981 ($\bar{X} = 41.3$ mm SVL) when the pond dried on days 167 and 116, respectively (Fig. 1).

Within-year variation in metamorphosis

In most years (1980, 1981, 1982, and 1983) the majority of larvae metamorphosed during <2 mo. How-

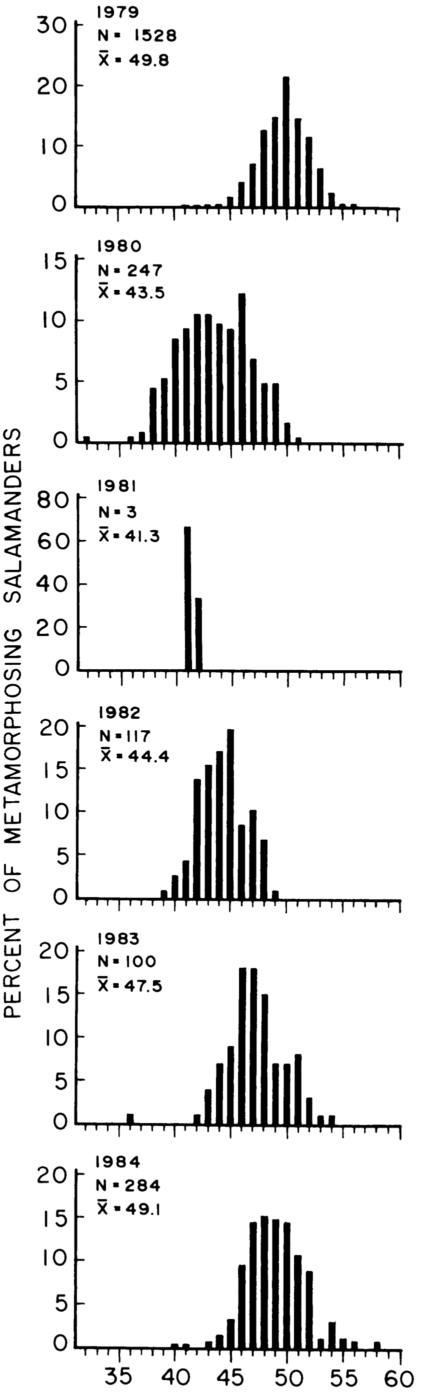

FIG. 1. Body size distributions of metamorphosing *Ambystoma talpoideum* from Rainbow Bay for 6 yr. Sample size and mean length are indicated for each year.

ever, during 1979 and 1984 when the pond dried late, >2000 larvae metamorphosed from June through October. There were natural breaks in the timing of metamorphosis between an early and a late group within these two years, despite a single breeding period. In 1979, 1412 newly metamorphosed juveniles emigrated between 7 and 22 July (early group, 35% of the total number) and 870 emigrated between 3 and 30 September (late group, 22%). In 1984, 4473 newly metamorphosed juveniles emigrated between 20 June and 31 July (early group, 37%) and 4510 emigrated between 28 September and 30 October (late group, 38%). Larvae that metamorphosed early were not significantly different in body size from those metamorphosing late in either year (1979: $t = 0.77$, df = 445, $P = .43$; 1984: $t = 1.07$, df = 248, $P = .29$; Table 1).

Body size at first reproduction

The majority of individuals metamorphosing from June through October returned to reproduce during the following breeding season (November–February) at 1 yr of age. Even though body size at metamorphosis of early and late groups did not differ significantly within a year, early metamorphs were significantly larger than late metamorphs at first reproduction. Early-metamorphosing males and females from 1979 were larger at first reproduction in 1980 than late-metamorphosing males and females ($t = 4.27$, df = 117, $P < .0002$; $t = 1.95$, df = 76, $P < .05$; respectively for sex; Table 1). Early-metamorphosing males from 1984 were larger at first reproduction in 1985 than late-metamorphosing males ($t = 4.14$, df = 125, $P < .0001$), but females were not significantly different ($t = 1.07$, df = 102, $P = .28$; Table 1). Early-metamorphosing males from 1984 reproducing at 2 yr of age in 1986 were also larger in body size ($\bar{X} = 57.3 \pm 0.2$ mm SVL) than late-metamorphosing males ($\bar{X} = 56.4 \pm 0.2$ mm SVL; $t = 3.42$, df = 428, $P < .0007$). Two-year-old females that metamorphosed early in 1984 were also significantly larger in 1986 ($\bar{X} = 56.8 \pm 0.2$ mm SVL) than late-meta-

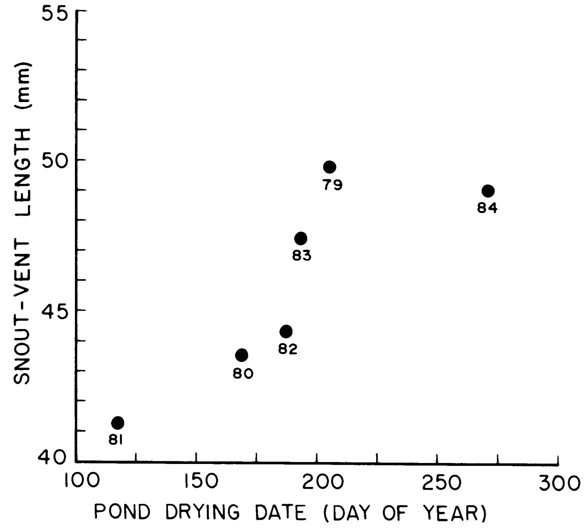

FIG. 2. Relationship between mean snout–vent length at metamorphosis for *Ambystoma talpoideum* and day of year of pond drying. Year is indicated for each data point.

TABLE 1. Body size at metamorphosis and at first reproduction for early- and late-metamorphosing *Ambystoma talpoideum* from 1979 and 1984 at Rainbow Bay ($\bar{X}$ ± 1 SE).

Year	Total number of metamorphs	Snout–vent length (mm)	
		At metamorphosis	At first reproduction
1979			
Early	1412	49.9 ± 0.06 $(N = 1090)$	Male 54.8 ± 0.26 $(N = 95)$
			Female 53.3 ± 0.30 $(N = 59)$
Late	870	49.8 ± 0.14 $(N = 238)$	Male 52.5 ± 0.46 $(N = 24)$
			Female 52.1 ± 0.55 $(N = 19)$
1984			
Early	4473	49.2 ± 0.19 $(N = 190)$	Male 53.0 ± 0.26 $(N = 111)$
			Female 51.2 ± 0.50 $(N = 38)$
Late	4510	48.8 ± 0.31 $(N = 60)$	Male 51.4 ± 0.28 $(N = 50)$
			Female 50.5 ± 0.40 $(N = 66)$

morphosing females ($\bar{X}$ = 55.8 ± 0.2 mm SVL; t = 3.49, df = 603, $P < .0005$).

We used an analysis of covariance for both sexes of the 1979 cohort to test separately the effects of time of metamorphosis and body size at metamorphosis on body size at first reproduction. We partitioned time into two levels (early and late) and used size at metamorphosis as the covariate. In both analyses the interaction term was not significant, indicating that slopes of the response variables were parallel, so the interaction sum of squares and degrees of freedom were incorporated into the residual error term. Both time of metamorphosis and size at metamorphosis had significant effects on body size at first reproduction for both males and females (Table 2). For any size at metamorphosis, larvae metamorphosing early attained a larger body size at first reproduction (2.3% larger for females and 4.3% larger for males) than those metamorphosing later in the season. In addition, larger metamorphosing individuals were also larger at first reproduction than those metamorphosing at a smaller size.

TABLE 2. Analysis of covariance for the effect of time (early and late) of metamorphosis and size at metamorphosis on size at first reproduction for male and female *Ambystoma talpoideum.* Body size at metamorphosis was the covariate in a Type III sum of squares model.

Source of variation	df	SS	MS	*F* ratio	*P* value
		Males			
Time	1	103.45	103.45	19.85	.0001
Size	1	140.39	140.39	26.94	.0001
Error	116	604.54	5.21		
Total	118	848.38			
		Females			
Time	1	27.22	22.72	6.42	.0134
Size	1	99.52	99.52	23.46	.0001
Error	75	318.22	4.24		
Total	77	444.96			

TABLE 3. Analysis of covariance for the effect of time (early and late) of metamorphosis and size at metamorphosis on age at first reproduction for male and female *Ambystoma talpoideum.* Body size at metamorphosis was the covariate in a Type III sum of squares model.

Source of variation	df	SS	MS	*F* ratio	*P* value
		Males			
Time	1	0.3085	0.3085	0.44	.5092
Size	1	1.5979	1.5979	2.27	.1343
Error	141	99.3157	0.7044		
Total	143	101.2221			
		Females			
Time	1	6.901	6.901	5.97	.0162
Size	1	9.790	9.790	8.48	.0044
Time × size	1	6.890	6.890	5.96	.0163
Error	108	124.820	1.156		
Total	111	148.400			

Age at first reproduction

Analysis of covariance for both sexes was used to assess the effect of time and size at metamorphosis on age at first reproduction (Table 3). Neither time of nor size at metamorphosis significantly affected age at first reproduction of males (Table 3). From the total number of early metamorphs in 1979 that survived and returned to Rainbow Bay during any subsequent year through 1984, 78% of the males reproduced for the first time at 1 yr of age and 22% reproduced for the first time at ages between 2 and 5 yr (Table 4). The majority of late male metamorphs (77%) also reproduced at 1 yr of age, with 23% reproducing at 2–5 yr of age (Table 4). A significant time-by-size interaction for females precluded interpretation of this test (Table 3). We therefore used regression analysis to examine the effects of size on age at first reproduction for early and late groups. For early-metamorphosing females, size at metamorphosis and age at first reproduction were negatively related (F = 21.2, df = 1,83, P = .0001, slope = −0.27); larger metamorphs returned to breed at a younger age. There was no significant relationship for late-metamorphosing females (F = 0.08, df = 1,25, P = .773, slope = −0.02). The majority of early-metamorphosing females (66%) reproduced at 1 yr of age with only 34% reproducing for the first time in subsequent years. Similarly, most late-metamorphosing females (68%) reproduced their 1st yr and 32% reproduced at 2–5 yr of age (Table 4).

TABLE 4. Number of adult *Ambystoma talpoideum* from the 1979 cohort of early- and late-metamorphosing juveniles that returned to reproduce in subsequent years. Proportions are given in parentheses.

Timing of metamorphosis	Number of marked metamorphs	Sex	Year of first reproduction*					Survival to first reproduction†
			1979–1980	1980–1981	1981–1982	1982–1983	1983–1984	
Early	1090	Male	95 (0.78)	4 (0.03)	8 (0.07)	6 (0.05)	8 (0.07)	121 (0.22)
		Female	59 (0.66)	1 (0.01)	11 (0.12)	14 (0.16)	5 (0.06)	90 (0.16)
Late	238	Male	24 (0.77)	1 (0.03)	5 (0.16)	1 (0.03)	0 (0.00)	31 (0.26)
		Female	19 (0.68)	1 (0.04)	5 (0.18)	2 (0.07)	1 (0.04)	28 (0.24)

* Proportion reproducing for the first time each year = number returning in year ÷ number returning during all years.

† Survival to reproduction = number returning during all years ÷ number of metamorphosed individuals, assuming a 1:1 sex ratio at metamorphosis.

Survival to first reproduction

The proportion of individually marked metamorphosing juveniles from 1979 that returned to reproduce for the first time between 1979 and 1984 (1–5 yr of age) was used to estimate survival. Based on the high degree of philopatry observed through mark-recapture studies at Rainbow Bay and at other directly adjacent breeding ponds, missing individuals most likely died rather than emigrated to another pond. The proportion of males that survived from the early group (22%) and the late group (26%) was not different ($G = 0.49$, df = 1, $P > .25$; Table 4). The proportion of females surviving from the early (16%) and late group (24%) also was not different ($G = 2.11$, df = 1, $P > .10$; Table 4). In addition, body size of metamorphosed individuals in four evenly divided size classes and survival to first reproduction were not significantly associated ($G = 1.68$, df = 3, $P > .50$; Table 5). Survival to first reproduction among the four size classes ranged from 18 to 22% of the marked metamorphosing juveniles.

DISCUSSION

These are the first data for salamanders that demonstrate that natural variation in timing of metamorphosis and body size at metamorphosis can influence size and age at first reproduction, traits closely associated with fitness. Earlier metamorphosis, after correcting for size at metamorphosis, led to larger size at first reproduction. Also, larger juveniles at metamorphosis led to larger adults at first reproduction for both sexes and younger age at first reproduction in females.

For *A. talpoideum,* both metamorphosing early and metamorphosing at a large size are advantageous. Except under very productive conditions, however, an individual larva must sacrifice one advantage for the other. Provided larval growth is positive, once a larva has reached the minimum size necessary to initiate metamorphosis it can either metamorphose early at a small size or late at a large size. The optimal trade-off between time and size at metamorphosis depends on how expected growth and survival for larvae compares with that for postmetamorphic juveniles. The relative advantages of remaining a larva compared with metamorphosing change temporally as larvae grow and their environment changes. Theoretical models for the optimal time and size of amphibian metamorphosis have been proposed by Wilbur and Collins (1973) and Werner (1986). Stearns and Koella's (1986) models of "reaction norms" for age and size at maturity can also be applied to this problem. Since we did not measure the growth and survival of larvae in this study, we cannot test these models explicitly. The positive correlations we observed between date of pond drying and both modal (and median or mean) date of metamorphosis and mean size at metamorphosis suggest, however, that in most years at Rainbow Bay the majority of *A. talpoideum* larvae delay metamorphosis until the pond begins to dry. This maximizes size at metamorphosis at the expense of early metamorphosis. When *A. talpoideum* larvae are subjected to experimentally ma-

TABLE 5. Survival to reproduction of marked metamorphosing juvenile *Ambystoma talpoideum* from the 1979 chort.

	Size classes at metamorphosis (mm)*			
	≤48.0	48.5–49.5	50.0–51.5	≥52.0
Number metamorphosing	311	240	485	292
Number surviving to reproduction	56	51	108	56
Proportion surviving to reproduction	0.180	0.212	0.223	0.192

* Individuals were placed in four size classes based on snout–vent length at metamorphosis, two classes above and two below the mean size for 1979 (49.8 mm SVL).

nipulated drying times in artificial ponds, metamorphosis is delayed until the pond is nearly dry (R. D. Semlitsch and H. M. Wilbur, *personal observation*).

In 1979 and 1984, the years the pond held water the longest, some larvae did not delay metamorphosis. There were two distinct pulses of metamorphosis. One group metamorphosed in June and July before the pond dried, while the other group metamorphosed in August and September, apparently stimulated by pond drying. The early and late groups did not differ in mean size at metamorphosis during either 1979 or 1984. Overall mean size at metamorphosis for 1979 and 1984 ranked first and second, respectively, among the 6 yr that any *A. talpoideum* metamorphosed at the pond.

In the 2 yr that Rainbow Bay dried late, the later metamorphosing individuals might have been in the lower half of the larval size distribution before the larger, early group metamorphosed. Although mean size at metamorphosis of the late group was not larger than that of the early group during either year, individuals in the late groups probably metamorphosed at a larger size than they would have, had they metamorphosed early. For individuals in the late group, conditions apparently favored delaying metamorphosis until they reached a larger size, similar to that attained by the early group. Individuals in the early groups may have reached the maximum size at metamorphosis for those environmental conditions (Wilbur and Collins 1973).

Timing of metamorphosis for *A. talpoideum* is further complicated by the fact that some individuals are facultatively paedomorphic (Semlitsch 1985*a*). This species can readily respond to constant water level conditions, abundant resources, and low density by delaying metamorphosis and becoming paedomorphic (Semlitsch 1987*b*). Individuals from the late groups in 1979 and 1984 had the opportunity to become paedomorphic if the pond did not dry. This option makes it very difficult to assess the relative benefits of early vs. late metamorphosis in this species. Under certain conditions, not metamorphosing at all might lead to higher survival, larger size at first reproduction, or earlier reproduction than either metamorphosing early or late (Semlitsch 1987*b, c*).

Larvae that metamorphose early achieve a larger body size at first reproduction but have the same probability of survival to first reproduction as larvae metamorphosing late. Because early and late metamorphs return to breed at nearly the same time, early metamorphs spend more time in the terrestrial environment. More time to forage and grow in the terrestrial environment or better foraging conditions early in the summer presumably accounts for the differences in body size between the two groups when they first return to reproduce, even when their body-sizes at metamorphosis were the same. This body-size advantage achieved during this 1st yr of life is maintained for at least a 2nd yr (e.g., 1984 metamorphs measured in 1985 and 1986). Presumably the body-size advantages are maintained for their entire lifetime (>6 yr for some individuals), whether the initial difference was because of timing of or size at metamorphosis. Thus, with the strong positive relationship of body size with egg number (Semlitsch 1985*a*, 1987*c*) and potentially with mating success, these advantages would affect an individual's lifetime fitness.

Although early metamorphs were larger at first reproduction than late metamorphs, the majority of growth took place prior to metamorphosis for both groups in both years. The minimum percentage of body size at first reproduction (snout–vent length) that was obtained at metamorphosis was 91% for early males in 1979. The largest percentage of body size obtained was 97% for both early and late females in 1984. Thus, an early-group male that hatched during March 1979, metamorphosed between 7 and 22 July 1979, and returned to breed for the first time in December 1979 would have achieved 91% of its growth in the first half of its life: the larval stage. For *A. talpoideum* it seems clear that growth in the larval aquatic environment is greater and thus probably more important than growth in the surrounding terrestrial environment. Some amphibians, however, do the majority of their growing in the terrestrial environment (Werner 1986). If maximizing growth in the aquatic stage were the most important consideration, we would expect *A. talpoideum* larvae to delay metamorphosis as long as possible. This does appear to be the pattern for *A. talpoideum* when pond drying is delayed, with the exception of the early-metamorphosing groups from 1979 and 1984. The potential benefit of delaying metamorphosis must always be weighed against the risk of desiccation in a drying pond (Shoop 1974).

Many experimental studies have documented the effects of competition and predation in the larval environment on growth, development, and survival to metamorphosis in amphibians (reviewed in Wilbur and Collins 1973, Wilbur 1980, and Morin 1983). The deficiency in these studies, however, has been the paucity of data on the relationship of these traits to the dynamics of natural populations. Berven and Gill (1983) found that *Rana sylvatica* in natural populations metamorphosing at a larger body size maintained that larger size at first reproduction and produced more eggs than small females. They also found that early-metamorphosing frogs had a significantly higher survival rate than late metamorphs. *Pseudacris triseriata* metamorphosing at a large body size maintained their size advantage at maturity (Smith 1987). Large body size and early metamorphosis in *P. triseriata* enhanced the chance that reproductive size was attained within 1 yr of metamorphosis but did not affect survival rate.

We have clearly demonstrated that phenotypic variation in the larval stage of *A. talpoideum* affects adult life history traits. This would suggest that factors associated with the spatial and temporal variation in reproduction (e.g., selection of oviposition sites, timing of reproduction) or larval growth (e.g., feeding, competitive ability, costs of predator avoidance) may affect adult fitness. More important, however, our data strongly suggest that an individual's lifetime fitness may also be affected by the larval environment.

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