

Life history of a small form of the plethodontid salamander *Desmognathus quadramaculatus*

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Abstract. We sampled *Desmognathus quadramaculatus*, one of the largest species of plethodontid salamanders in eastern North America, from a population exhibiting extremely small adult body sizes in the Bald Mountains of North Carolina (USA). In order to test the hypothesis that miniaturization in desmognathine salamanders is due to early metamorphosis and maturation, we estimated ages and sizes at metamorphosis and maturation. Analysis of size-frequency distributions suggests that most larvae metamorphose after 24 months, with the remainder metamorphosing after 36. The minimum age of sexually mature individuals in the summer months is estimated to be 4 years in males and 5 years in females; some may mature 1 year earlier. This is earlier than other reliable estimates of age at maturation in *D. quadramaculatus*, and appears to account for the small size of the species at this locality. Larval and juvenile growth rates are within the range of growth rates of other populations. As in other populations of *D. quadramaculatus*, males are smaller than females at maturation, but grow to larger sizes. Estimates of clutch sizes based on dissection of gravid females are relatively low. The other species of salamanders in this community do not appear to be miniaturized.

Introduction

The salamander family Plethodontidae is well known for its wealth of species and diversity in ecology and life history. The eastern North American genus *Desmognathus* in particular has been investigated intensively because these species covary among larval period, metamorphic size, adult body size, and habitat use. Large species, e.g., *D. quadramaculatus* (Holbrook, 1840), have lengthy larval periods, large metamorphic sizes, and delayed maturation when compared with smaller congeners, e.g., *D. monticola* Dunn, 1916 and *D. ocoee* Nicholls, 1949 (Bruce, 1988, 1989). This pattern of covariation within *Desmognathus* has generally been thought to represent a microcosm of two general evolutionary trends found in the entire family: (1) phylogenetic reduction in body size (i.e., miniaturization sensu Hanken and Wake, 1993), and (2) evolution of direct development (Wake, 1966;

Wake and Hanken, 1996). These trends have been the subject of scrutiny because body size is the most obvious feature of animals that is relevant to evolutionary ecology, and direct development is the usual pathway in amphibians to emancipation from the aquatic larval environment (Dunn, 1926; Titus and Larson, 1996; Wake and Hanken, 1996).

While the morphological and ecological consequences of miniaturization in amphibians (and plethodontids in particular) are well known (Hanken, 1983, 1985; Hairston, 1986; Resetarits, 1991; Formanowicz and Brodie, 1993; Hanken and Wake, 1993; Beachy, 1994; Rose, 1996; Beachy, 1997), the causes of this trend are not. Age at maturation covaries with size in *D. ocoee*, *D. monticola* and *D. quadramaculatus* (Tilley, 1973, 1980; Bruce, 1988; Bruce and Hairston, 1990; Castanet et al., 1996; Bruce et al., 2002) and appears to explain much of the interspecific variation in plethodontid body size (Houck, 1977a; Tilley and Bernardo, 1993; Beachy, 1995a; Ryan and Bruce, 2000). In addition to maturation age, there are several other traits that can covary with adult body size: egg size (with consequent effects on hatchling size), metamorphic size, metamorphic age, and maturation size (Beachy, 1995a). We explored which of these traits seems most associated with the very small size of individuals in an unusual population of *D. quadramaculatus*.

Throughout its range, *D. quadramaculatus* tends to be the largest member of local desmognathine assemblages (Organ, 1961; Hairston, 1986), and among the largest species of the plethodontid salamander fauna (Petranka, 1998). However, in 1995, in visiting a tributary of Shelton Laurel Creek in the Bald Mountains, North Carolina, we found a population of *D. quadramaculatus* that contained what appeared to be the smallest mature specimens on record. The discovery of the Bald Mountains population represented an opportunity to test the hypothesis that reduction in adult body size in plethodontids is a result of precocious metamorphosis and maturation (Bruce, 1988; Beachy, 1995a). The larval period, size at metamorphosis, and age and size at maturation are known to vary considerably in this species (Organ, 1961; Bruce, 1985, 1988; Austin and Camp, 1992; Camp et al., 2000). The objective of the present study was to evaluate the “precocious-threshold hypothesis” based on analysis of seasonal variation in the distributions of body sizes and life-history stages in the Bald Mountain population of *D. quadramaculatus*.

Materials and methods

The site, Gott Farm Creek, is a tributary of Shelton Laurel Creek in the Bald Mountains (35°58'05"N, 82°41'40"W, White Rock quadrangle), Madison County, NC. Gott Farm Creek is a typical southern Appalachian headwater stream. The bottom is a heterogeneous mix of large rocks, cobble, gravel, sand, and silt, with an alternation of riffles and pools. The pools are generally <20 cm deep, and the riffles vary from 2 cm to 10 cm in depth. At this site, *D. quadramaculatus* is the most abundant salamander, but other typical southern Appalachian stream salamanders occur, including *D. marmoratus* Moore, 1899, *D. monticola*, *D. orestes* Tilley and Mahoney, 1996, *Eurycea wilderae* Dunn, 1920, *Pseudotriton ruber* (Sonnini, 1802), and *Gyrinophilus porphyriticus* (Green, 1827). Throughout the sampling area there are no fish. The density of *D. quadramaculatus* at Gott Farm Creek is greater than we have experienced at any other location. Our field trips never resulted in fewer than 26 individuals per person-hour.

The middle part of Gott Farm Creek flows through a cow pasture bordered by a narrow zone of shrubs and trees; the upper and lower sections of the sampling area descend through cove forest dominated by Canadian hemlock (*Tsuga canadensis*) and hardwoods, with dense understory of rhododendron (*Rhododendron maximum*). Our collections were made at elevations between 730 and 790 m.

The salamanders were collected either by hand or with a D-frame dipnet (setting the net below a riffle and disturbing the rock and gravel above). Samples were collected in mid July 1997, mid June and early October 1998, and in early May 1999. Except for the June 1998 sample, the specimens were killed by prolonged immersion in a 1% solution of aminobenzoic acid ethyl ester (MS-222), preserved in a 10% formalin solution, and stored in ethanol (70%). These animals were deposited in the Minot State University vertebrate collections. The salamanders of the June 1998 sample were anesthetized in a 1% MS-222 solution to facilitate measurement, then revived in stream water and returned to the site of collection. The decision to release was predicated by our initial concern for depleting what appeared to be a very restricted, unique population of *D. quadramaculatus*. This concern was allayed by later observations, and the specimens taken in October 1998 and May 1999 were all preserved.

Several brooding females were observed in July 1997. One brooding female was collected with her clutch of 32 eggs and brought to the laboratory, where the eggs were maintained until hatching to obtain estimates of hatching size.

All salamanders were measured (length in mm, from tip of snout to posterior margin of the cloacal vent [SVL]) and scored as either larva, metamorphosing larva, or metamorphosed individual. Sex and reproductive status of metamorphosed individuals were determined for preserved animals. Males with small testes and straight, narrow, unpigmented vasa deferentia were considered immature. Mature males possessed enlarged, lightly pigmented testes, and black, coiled vasa deferentia. Females were considered mature if the ovarian follicles showed evidence of vitellogenesis, and if the oviducts were wide and either sinuous or convoluted, versus narrow and straight in immatures. We measured salamanders in 1997 after preservation, and those of the later samples before preservation. Shrinkage that accompanies preservation is about 5-7% of SVL; this difference was considered in comparing the 1997 and later samples.

We estimated age structure by using histogram analysis of body size distributions. This method depends on knowledge of the age of the smallest size class combined with large samples to clarify size modes in an age-structured population (e.g., Halliday and Verrell, 1988; Russell et al., 1996). Because the new hatchling age class in biphasic plethodontids (i.e., the desmognathines and hemidactyliines) can often be clearly identified (and because this and older cohorts can be followed in subsequent samples through the yearly cycle), this technique has been used frequently to estimate age at metamorphosis and maturation in plethodontids (e.g., Houck, 1977b; Voss, 1993; Ryan, 1998). Furthermore, use of size-frequency distributions has been shown to be an accurate estimator of metamorphic and maturation ages in desmognathine salamanders, yielding results that have been confirmed with skeletochronological methods (Castanet et al., 1996; Bruce et al., 2002). Growth rates were estimated using the general formula $[(L_{x+1} - L_x)/(t_{x+1} - t_x)]$ where t_{x+1} and t_x are different times and L_{x+1} and L_x are measurements of body size taken at those times. The mode of each larval age class was used to estimate L_x at each t_x .

Results

Larval period and metamorphosis. Several females attending clutches were observed during the July 1997 collection. Eggs were found attached in a monolayer to the underside of large flat rocks. Coupled with the appearance of small larvae in the October 1998 sample, these observations suggest that oviposition occurs in early to mid summer, with hatching following in late summer and early fall. Only three embryos from the collected clutch survived until hatching (in early September), each 13 or 14 mm SVL. This limited data set indicates that hatching size at Gott Farm Creek is similar to that reported elsewhere (Pope, 1924; Organ, 1961; Bruce, 1985, 1988). We follow Organ (1961) and Bruce (1988)

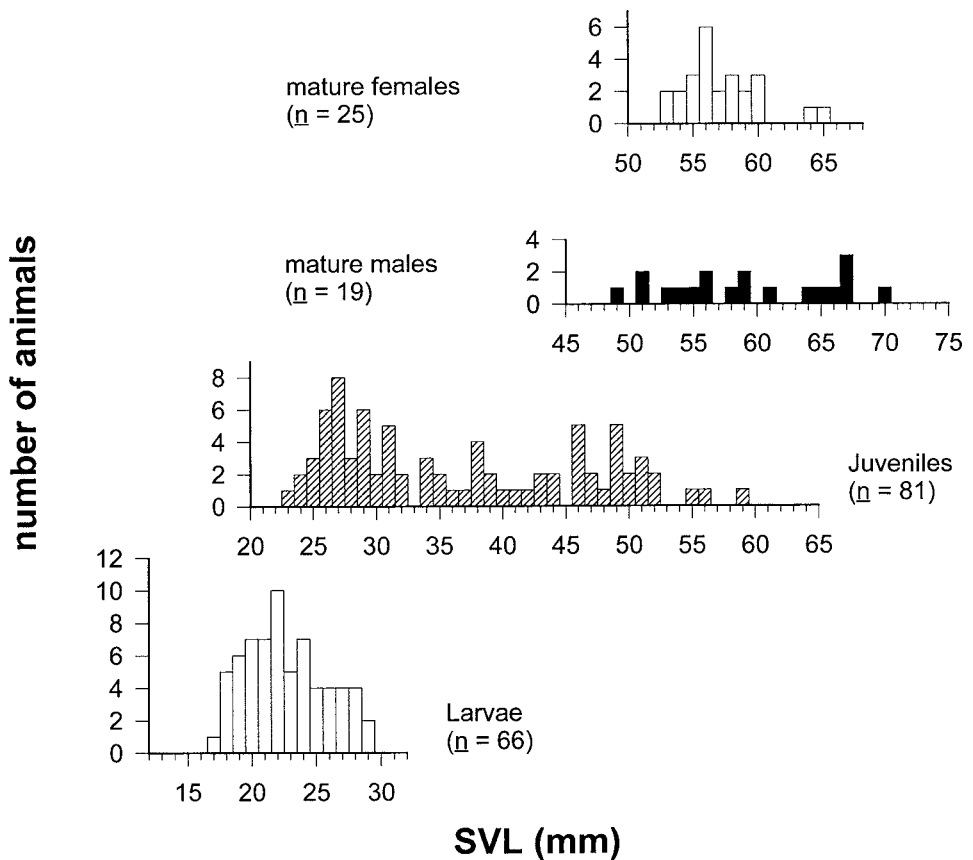


Figure 1. Snout-vent length distributions of formalin preserved larvae, juveniles, and adults of *Desmognathus quadramaculatus* taken at Gott Farm Creek, July 1997.

in estimating age from the month that an individual enters the population as an egg, which we estimate to be June at Gott Farm Creek.

Because hatchlings had not yet appeared in the July 1997 sample, the smallest larvae are estimated to be 13 months old (fig. 1). The size distribution of larvae appeared unimodal, indicative of a single age class, yet the range in SVL (17-29 mm) was considerable, and the overlap in SVL of larvae and metamorphosed juveniles (23-29 mm) was extensive. Thus, although it was difficult to determine age at metamorphosis from this sample alone, we estimate that the larval component of the sample consisted of either 13-month old larvae or (more likely) a mixture of 13-month old and 25-month old individuals.

Metamorphosis apparently occurs in early to mid summer. Several larvae were present in June 1998 that exhibited reduction of labial folds and external gills. In contrast to the July sample of the year before, the SVL distribution of larvae in June 1998 tended toward bimodality, indicative of two age classes, representing 12-month old larvae and either 24-

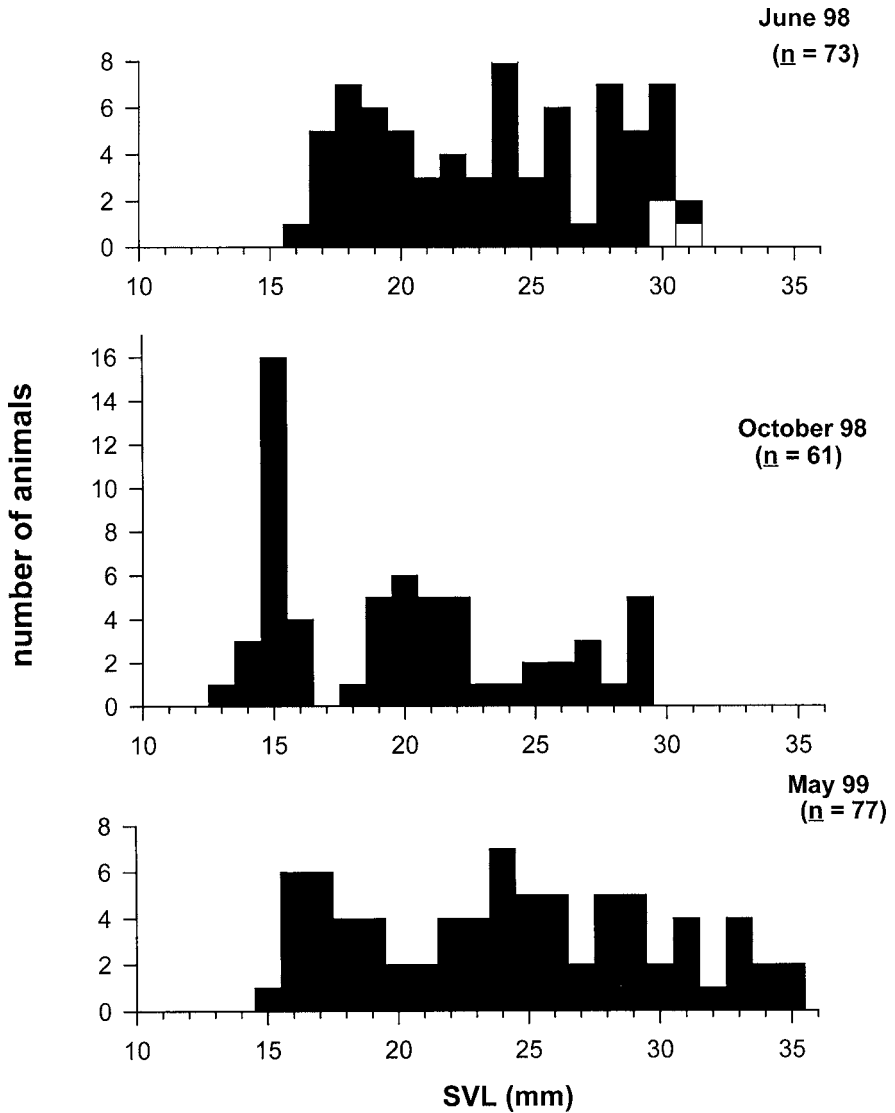


Figure 2. Snout-vent length distributions of live-measured larvae of *Desmognathus quadramaculatus* taken at Gott Farm Creek, June 1998 – May 1999. Open bars are metamorphosing larvae.

month old larvae or a mix of 24-month old and 36-month old larvae (fig. 2). There was again a broad overlap in size (from 24 to 31 mm) of larger larvae and smaller juveniles. The three metamorphosing individuals in this sample were estimated to be either 24 or 36 months old, probably the latter. It seems likely that any 36-month old larvae present in the population in early summer would metamorphose during the current metamorphic season.

In the October 1998 sample, the hatchlings of the current year, now aged 4 months, formed a discrete class of small larvae, with a mode at 15 mm (fig. 2). The larger larvae in the October sample appear to sort into two age classes of 16- and 28-month old individuals, with a lower frequency of the latter cohort than in the June sample taken four months earlier. This decrease probably reflected losses via metamorphosis of all 3-year old and some 2-year old larvae during summer.

By early May 1999 there had been a marked upward shift in SVLs of all three age classes identified in October (fig. 2). The boundary between the 23- and 35-month old larvae was obscure, but that between the 11- and 23-month old age classes was still evident. This sample contained the largest larvae of any of the samples, which was expected if metamorphosis occurs from early to mid summer.

The broad size overlap between larvae and juveniles in both July 1997 and June and October 1998 suggests that larvae metamorphose after 24 or 36 months. It was difficult to estimate the proportions metamorphosing at either age, but the large number of juveniles <30 mm, especially in July 1997, indicates that the frequency of metamorphosis at the earlier age of 24 months is relatively high. The break in SVL between 11- and 23-month old larvae at 20-21 mm in the May 1999 sample suggests that the tiny juveniles (23-25 mm) in the June and July samples of earlier years were at least 24 months of age.

In summary, the data of the complete set of samples support the conclusion that many larvae metamorphose at 2 years of age, with the remainder transforming at 3 years of age. A relatively high frequency of early metamorphosis at 2 years would account for the prevalence of tiny juveniles in this population. We cannot discount the hypothesis that some of the latter derive from fast-growing larvae that metamorphose as early as 12 months of age.

Larval growth rates. Growth rates were inferred by examining the modal size of each larval age class. This cross-sectional approach generated estimates for intervals between the first and second age classes and between the second and third age classes (table 1). These interval estimates were similar to the values obtained by examining the change in modal size for each cohort from the October 98 sample to the May 99 sample. Thus, the cross-sectional estimates of larval growth were used as a basis for comparing the monthly growth rates (table 1). These values ranged from 0.42 to 0.63 mm SVL per month for growth during the first year of larval growth, and from 0.50 to 0.75 for the second year. When compared with estimates of larval growth rates generated from the data of Bruce (1988) and Austin and Camp (1992), it appears that the rate of larval growth at Gott Farm Creek is of the same order as other populations (table 1).

Age at first reproduction/maturation. The SVL distribution of juveniles in the July 1997 sample (fig. 1) suggests at least two size/age classes, with larger juveniles broadly overlapping adults in size. Based on our interpretation of the larval size distributions, the smaller juvenile class would include 25- and 37-month old individuals, including some of those equaling or exceeding 35 mm SVL. The class of older juveniles would include 37-

Table 1. Summary of body sizes of larval age classes and estimates of larval growth rate of *Desmognathus quadramaculatus* from Gott Farm Creek (and four other localities). The body size data are estimated from the mode of each age class identified in fig. 2. Larval growth rates are estimated by assessing the change in SVL from one age class to the next and dividing by 12 months. The intervals refer to the time between one age class and the next, e.g., a population with two intervals has a three year larval period.

Larval body sizes (mm SVL)		Age class			
Sample		1	2	3	4
June 98		–	18.0	24.0	29.0
October 98		15.0	20.0	29.0	–
May 99		16.5	24.0	31.0	–

Larval growth rates (mm SVL/mo). Data are means (<i>s</i>)					
	Gott Farm Creek ^a	Highlands ^b	Coweeta ^b	Wolf Creek ^b	Nancy Town Creek ^c
Interval 1	0.52 (0.15)	0.47 (0.07)	0.51 (0.01)	0.48 (0.03)	1.02 (0.08)
Interval 2	0.61 (0.13)	0.54 (0.06)	0.62 (0.03)	0.58 (0.06)	0.54 (0.06)
Interval 3	–	0.69 (0.13)	0.62 (0.01)	–	–

^a this study; all animals complete metamorphosis by 3 years.
^b Bruce (1988): animals from Highlands and Coweeta metamorphose after 3 or 4 years, whereas all animals from Wolf Creek complete metamorphosis by 3 years.
^c Austin and Camp (1992): all animals metamorphose at 3 years of age.

and 49-month old and any older immatures. The broader range of size overlap between immatures and males, in contrast to females, indicates that males mature earlier than females. Thus, the youngest males in the July 1997 sample might be 49 months old and the youngest females at least one year older (61 months). However, it is likely that age at maturation varies in both sexes, with overlap between sexes, as in other desmognathines (Castanet et al., 1996; Bruce et al., 2002).

Specimens in the June 1998 sample were not dissected, and in any case the number of large, presumably adult, individuals was small in this sample. The size distributions in the samples of October 1998 and May 1999 suggest the presence of no more than a single size class of immature males, but presumably including mixes of 28- and 40-month old (October) and 35- and 47-month old (May) individuals (fig. 3). The maximum size of immature females (54 mm) was greater than that of such males (42 mm) in these samples, again indicating an earlier age at maturation in the latter sex. Thus the data of the 1998-99 samples were concordant with those of the single 1997 sample, in support of the conclusion that males attain maturity as early as 4 years and females at 5 years in this population. It is conceivable that animals that metamorphose after only 2 years could mature 1 year earlier than these estimates.

Sexual size dimorphism. In the three samples in which the specimens were preserved and dissected, we found that males attained sexual maturity at smaller sizes than females, but grew to larger sizes (table 2). Thus the size range of adult females was considerably

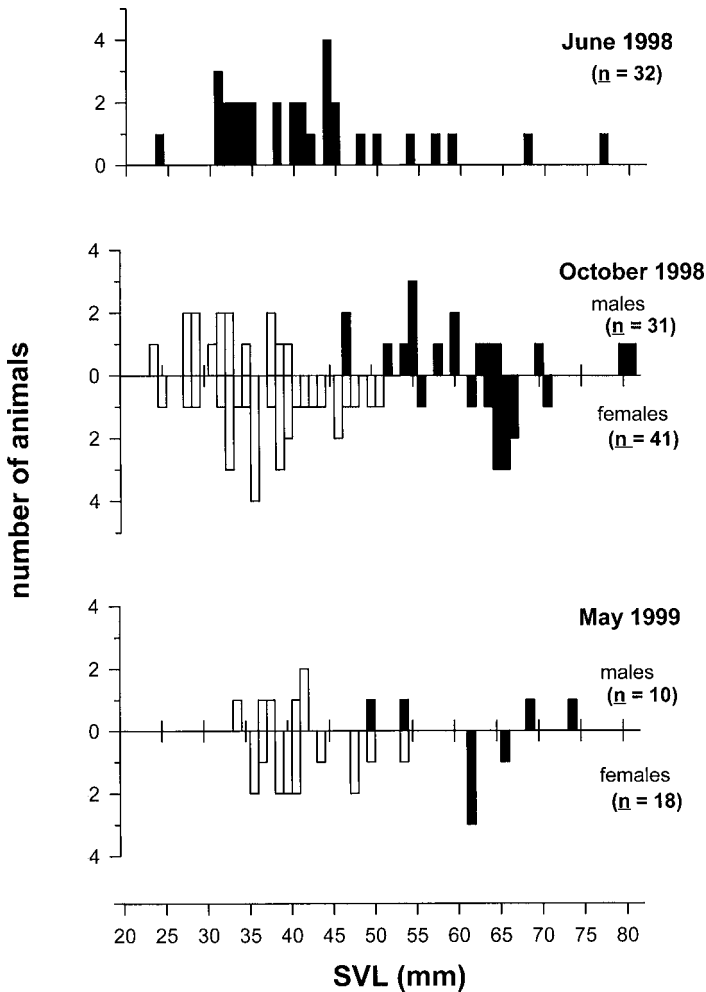


Figure 3. Snout-vent length distributions of live-measured juveniles (open bars) and adults (filled bars) of *Desmognathus quadramaculatus* taken at Gott Farm Creek, June 1998 – May 1999. Animals from the June 1998 sample were not dissected and assessed for sex and reproductive status.

narrower than that of adult males. Although the mean sizes of males and females were similar, the variances of SVL were significantly greater in males in all three comparisons (table 2). This is a consistent pattern in desmognathine salamanders (Bruce, 1993, 2000).

Juvenile growth rate. Juvenile growth rates were estimated by assuming a 12 mo juvenile period for males and a 24 mo juvenile period for females, and dividing the size increase from metamorphosis to maturation by these figures (table 3). As with larval growth, the juvenile growth rates calculated for each sex at Gott Farm Creek were within the range observed in the populations studied by Bruce (1988).

Table 2. Body sizes of sexually mature *Desmognathus quadramaculatus* at Gott Farm Creek.

Date	Sex	n	SVL (mm) ¹		s	F _s	Variance Test	
			Range	Mean			df	P
July 1997	M	19	49.5-70.9	59.9	6.44			
	F	25	53.2-65.5	57.7	3.06	4.43	18, 24	<0.002
October 1998	M	15	47.2-80.8	61.0	9.64			
	F	12	56.4-70.6	64.9	3.43	7.89	14, 11	<0.002
May 1999	M	4	50.3-73.6	61.8	11.31			
	F	4	62.2-66.0	63.2	1.87	36.64	3, 3	<0.02

¹ July 1997 data taken on preserved specimens. October 1998 and May 1999 data taken on living (anesthetized) salamanders.

Table 3. Ages and sizes at maturation and juvenile growth rates of *Desmognathus quadramaculatus* from Gott Farm Creek and three other localities.

	Gott Farm Creek ^a	Highlands ^b	Coweeta ^b	Wolf Creek ^b
Males				
Age at maturation (mo)	48	72	72	72
Size at maturation (mm SVL)	44	57	57	57
Duration of juvenile period (mo)	12	12	12	24
Size at metamorphosis (mm SVL)	30	40	41	36
Juvenile growth rate (mm SVL/mo)	1.17	1.42	1.33	0.88
Females				
Age at maturation (mo)	60	84	84	84
Size at maturation (mm SVL)	55	73	73	73
Duration of juvenile period (mo)	24	24	24	36
Size at metamorphosis (mm SVL)	30	40	41	36
Juvenile growth rate (mm SVL/mo)	1.04	1.03	1.33	1.03

^a this study.

^b Bruce, 1988.

Fecundity. Ten females (62-71 mm SVL) in the October 1998 sample were gravid, having large, yolked ovarian follicles, presumably earmarked for the clutch of eggs to be oviposited in the next summer. Counts of the yolked follicles ranged from 30 to 46 (mean ± s = 38.0 ± 6.11). The slope of the regression of follicle number on SVL was non-significant (F_{1,8} = 2.21, P = 0.176). Thus, we detected no tendency for follicle number or clutch size to increase with body size. This may reflect the narrow range of body size in adult females combined with the influence of other factors on fecundity.

Other desmognathines at Gott Farm Creek. The three other species of *Desmognathus* observed at Gott Farm Creek showed no evidence of miniaturization. The largest specimens in our small samples were 70 mm in *D. marmoratus* (n = 4), 70 mm in *D. monticola* (n = 17), and 35 mm in *D. orestes* (n = 12). We suspect that additional sampling of all three species would extend the size range upward. The former two species may equal or

exceed *D. quadramaculatus* in body size. The small numbers of these other species is in part a consequence of our emphasis on *D. quadramaculatus*, but also reflects their relative scarcity at Gott Farm Creek.

Discussion

Larval *D. quadramaculatus* at Gott Farm Creek grow slowly, as in most species of stream-dwelling plethodontids, and metamorphose after two or three years. A juvenile period of one year for males and two years for females supports a conservative estimate of 48 months (for males) and 60 months (for females) for age at first reproduction/maturation (maturation one year earlier may also be possible for larvae metamorphosing after two years).

All other estimates of minimal size at first reproduction/maturation in *D. quadramaculatus* are larger (Organ, 1961; Bruce, 1988; Castanet et al., 1996; Camp et al., 2000; Bruce and Castanet, 2002), as are all other estimates of minimal size at metamorphosis (Organ, 1961; Bruce, 1988; Austin and Camp, 1992; Camp et al., 2000). Based on these comparisons and other available data (Petranka, 1998; Camp et al., 2000), we consider the population of *D. quadramaculatus* at Gott Farm Creek to represent a case of body size reduction. Given the similarity in hatchling size and larval and juvenile growth rates at Gott Farm Creek compared to estimates from other populations, we suggest that the small size at Gott Farm Creek is principally due to precocious metamorphosis and maturation. Reduction in body size via early metamorphosis and/or maturation appears to be the pattern for desmognathines and in salamanders in general: several species of *Triturus* exhibit body size reduction relative to sister species by acceleration of gonadal development (Caetano and Castanet, 1993; Diaz-Paniagua et al., 1996; Denoel and Joly, 2000).

Variation in metamorphic age is often attributed to larval growth history (Wilbur and Collins, 1973; Werner, 1986). Differences in larval growth rate have been shown to affect metamorphic timing in fish, frogs, ambystomatid salamanders, insects and crustaceans (Alford and Harris, 1988; Alford, 1999; Beachy et al., 1999; Harris, 1999; Hentschel, 1999; Ryan, 2000; Beachy, 2001). However, larval development and growth are decoupled in plethodontids: variation in growth rate does not result in variation in metamorphic timing (Beachy, 1995b, 1997; O'Laughlin and Harris, 2000). Clearly, rapid larval growth can have consequences for increases in metamorphic and maturation size in plethodontids (Ryan, 1998; Camp et al., 2000), but it fails to affect metamorphic timing.

Early metamorphosis could be a thermal phenomenon. Warmer temperatures lead to earlier metamorphosis in salamander larvae (Uhlenhuth, 1919; Beachy, 1995b). In contrast, lower temperature is thought to result in later oviposition (Bruce, 1982; Voss, 1993; Ryan, 1998), with a consequent effect of later hatching and later metamorphosis at larger size (Beachy, 1995b). There are few direct temperature data on the habitats occupied by larval plethodontids and the general assumption is a correlation of elevation and temperature (Camp et al., 2000), but Voss (1993) has shown that it is the thermal variation associated

with stream order (rather than elevation) that results in variation in age at metamorphosis in plethodontid larvae. Unfortunately, except for Voss (1993), data on specific stream temperature regimes experienced by plethodontid larvae are lacking.

Precocious maturation could also be an effect of thermal regimes. High elevation *D. carolinensis* and *D. ocoee* (Tilley, 1973, 1980) mature later and at larger sizes, and duration of growth/development seasons is often invoked to explain the delay in maturation in environments with a smaller annual thermal budget (e.g., Smith-Gill and Berven, 1979). However, the variation in life history in *D. ocoee* is not due to thermal effects: the difference in maturation rate is preserved in reciprocal transplants (Bernardo, 1994). Thus, the accelerated maturation of Gott Farm Creek *D. quadramaculatus* may be unrelated to the thermal correlates of elevational differences.

Variation in maturation age in desmognathines has been explained in several ways that argue for either age at maturation or adult body size as local adaptation. Bernardo (1994) suggested that, aside from large size as a consequence of delayed maturation, there is selection at high elevation sites for increased egg size to favor larval overwintering at these sites with shorter growth seasons. For salamanders, egg size is larger in larger females (Kusano, 1982; Semlitsch and Gibbons, 1990; Bernardo, 1994). Bernardo (1994) suggested a model wherein body size is a correlated effect of selection on increasing egg size, which in turn is thought to increase larval survival over the first winter. Thus, there is relaxed selection on large egg size at lower elevations due to milder thermal conditions.

A final issue is simultaneous consideration of the accelerated thresholds, i.e., metamorphosis and maturation. Endocrine models suggest that some linkage must exist because the hormone systems involved in control of each threshold may antagonize the action of the other (Wakahara, 1994; Ryan, 2000). For plethodontids, the linkage must not be a restrictive one. Age at maturation can remain the same regardless of variation in metamorphic age in *D. quadramaculatus* (Bruce, 1988), and age at maturation can vary among populations of *G. porphyriticus* that probably metamorphose at the same age (Bruce, 1972, 1978). The clearest evidence that the two thresholds can evolve independently is the presence of paedomorphic plethodontid salamanders that forego metamorphosis altogether (e.g., Petranka, 1998; Ryan and Bruce, 2000). Both thresholds are worth exploring, however we cautiously interpret age at maturation as the pertinent accelerated parameter. Reduction in larval period may simply be a spurious correlate of accelerated maturation. Barring neoteny, metamorphosis must precede maturation. This means that in the occurrence of accelerated maturation, metamorphosis must also be accelerated.

In summary, the small size of *D. quadramaculatus* at Gott Farm Creek is due to accelerated maturation and (to a lesser degree) metamorphosis. This acceleration regime is likely to have several possible sources. At present, we do not understand the causal factors responsible for acceleration and small size in the Gott Farm Creek population of *D. quadramaculatus* (or any other population of plethodontid). The paucity of mortality schedules for plethodontids remains problematic in understanding plethodontid life histories. Resolution of this problem and application of thoughtful experimental life history analyses (e.g.,

Bernardo, 1994) promise important breakthroughs in understanding the evolution of these salamanders in particular and for age-structured populations in general.

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