

## Life-History Correlates of Body-Size Differences Between Two Populations of the Salamander, *Desmognathus monticola*

RICHARD C. BRUCE<sup>1</sup> AND NELSON G. HAIRSTON, SR.<sup>2</sup>

<sup>1</sup>Highlands Biological Station, P.O. Box 580, Highlands, North Carolina 28741, USA, and  
Department of Biology, Western Carolina University, Cullowhee, North Carolina 28723, USA

<sup>2</sup>Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, North Carolina 27514, USA

**ABSTRACT.**— We compare samples of *Desmognathus monticola* taken independently at two nearby localities in southwestern North Carolina. Larger adult body sizes are attained by both sexes at Coweeta Hydrologic Laboratory in the Nantahala Mountains than at Wolf Creek in the Cowee Mountains. The juvenile period appears to be longer in the former population, resulting in larger sizes at maturation in both males and females. The proportion of older males is greater at Coweeta than at Wolf Creek, suggesting higher male survival in the former population. Clutch sizes are lower at Coweeta than at Wolf Creek, even though Coweeta females are larger. We suggest that the population differences in body size may represent differences in age at maturation rather than differences in growth rates. The pattern of variation in life history parameters suggests that extrinsic survival probabilities differ between the sites, with Coweeta representing a safer environment for *D. monticola* than Wolf Creek.

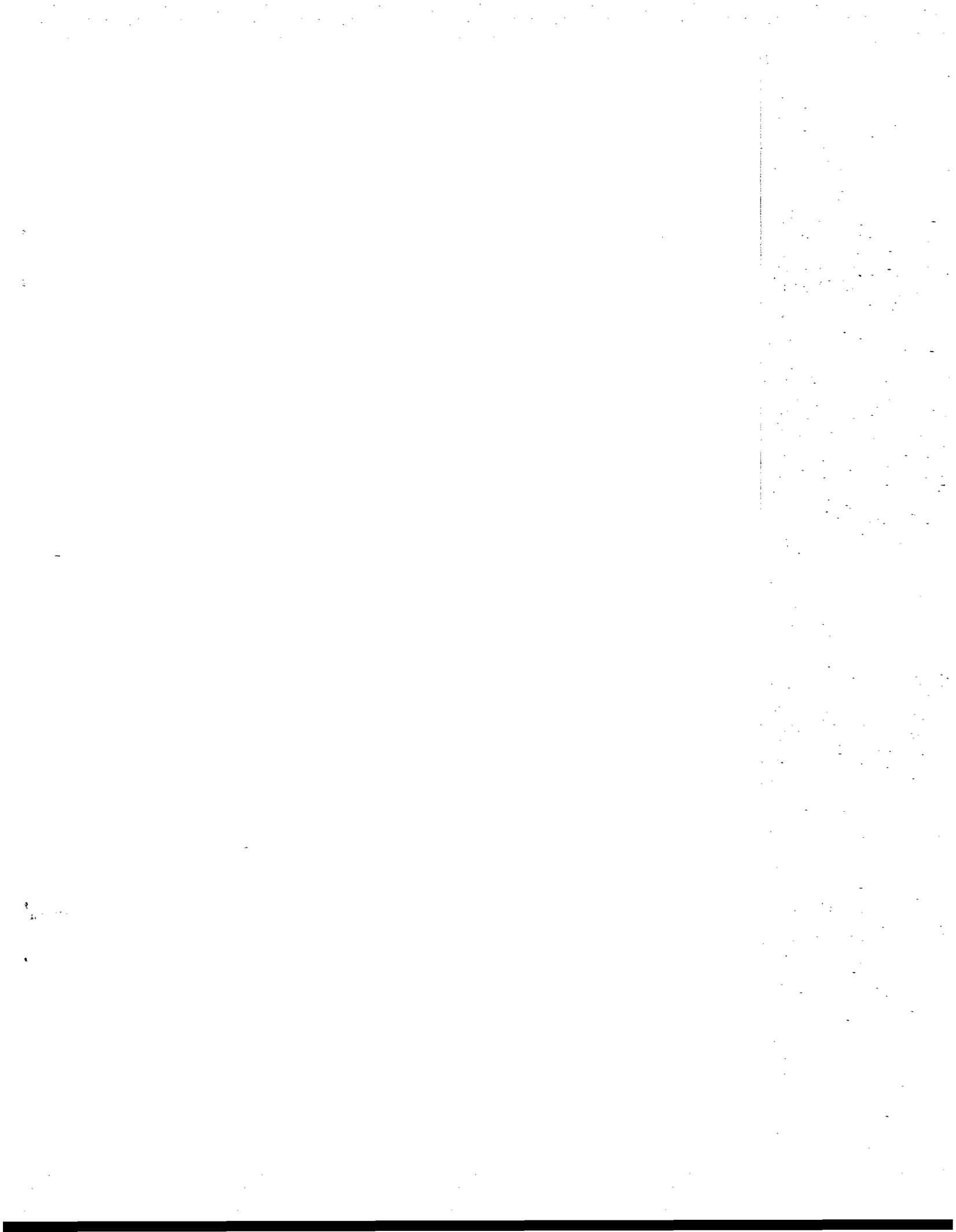
Multispecies communities of streamside salamanders of the genus *Desmognathus* are important components of southern Appalachian forest ecosystems. The member species, usually 3-5 in any one community out of a total pool of nine Appalachian species, show a gradation in adult body size which is strictly correlated with habitat preference and morphology: larger species are more aquatic and smaller ones are more terrestrial. Competition and predation have been identified as the factors responsible for the origin and persistence of community structure in *Desmognathus*, with predation apparently having the greater role (Hairston, 1986, 1987).

Among desmognathine communities, the same gradient in body size always occurs; i.e., *D. quadramaculatus* is invariably larger than *D. monticola*, the latter is always larger than *D. ochrophaeus*, etc. Yet there is geographic variation within species. For example, Tilley (1977, 1980) found that adult body-size differences were attributable to variation in growth and age at maturity in two nearby rock-face populations of

*D. ochrophaeus*. His two populations were separated by 424 m in elevation. The question remained whether the observed difference reflected direct environmental effects or evolutionary divergence of the two populations.

Working independently, we sampled different but nearby populations of *Desmognathus monticola* in the southern Blue Ridge Mountains of southwestern North Carolina. Body-size and life-history data were recorded by each of us. RCB's studies were directed toward life-history comparisons of *D. monticola* and *D. ochrophaeus* (Bruce, 1989, 1990). NGH investigated ecological interactions in the whole *Desmognathus* community (Hairston, 1986). In comparing our two data sets, we noted a pronounced difference in adult body size. We thought it would be of interest to quantify and evaluate the difference in the context of the available life-history data.

In designing the analyses to be conducted, two hypotheses seemed reasonable. First, the body-size difference might reflect direct environmental influences on growth. Direct envi-



ronmental effects on growth rate represent the most parsimonious explanation of body-size differences if size varies in accordance with some environmental gradient (Sebens, 1987). Alternatively, the difference in size might represent evolved responses of life-history parameters to environmental differences between the two habitats. Age at maturation and reproductive effort influence growth and adult body size, and are expected to respond jointly to selective pressures (Stearns and Crandall, 1981). Some combination of environmental effects and genetic divergence might be involved. Since we both collected data pertaining to growth, maturation, and fecundity, the information essential for examining these questions was available.

#### MATERIALS AND METHODS

NGH's samples were taken in May–September, 1981–1984, in and along several tributaries of Shope Fork at the Coweeta Hydrologic Laboratory in the Nantahala Mountains, Macon County, North Carolina. The streams, in numbered watersheds 31, 34, and the confluence of 40 and 41, flow E and SE. The sections sampled lie at elevations between 868 and 914 m.

The samples taken by RCB were collected from May 1985 through August 1988 in the watershed of Wolf Creek, on Cullowhee Mountain in the Cowee Mountains, Jackson County, North Carolina. Wolf Creek flows to the NW. The samples were taken at elevations between 800 and 1100 m, but mainly above 900 m.

Both study areas lie within mature deciduous forests, which often have dense thickets of *Rhododendron maximum* along the streams. Precipitation at Coweeta (>200 cm) is higher than at Wolf Creek (~150 cm). Wolf Creek is approximately 27 km NE of Coweeta.

The Coweeta samples were taken as part of an experiment involving removal of specimens from experimental plots (Hairston, 1986). Most of the collecting was done at night without disturbing cover objects. The specimens were returned to the laboratory, held overnight in a refrigerator, anesthetized in Chloretone, laid out on a clear glass plate together with a clear plastic ruler under a wet towel, and photographed from below with Panatomic X film. Glossy prints (8 × 10") were made, and the images of the rulers were cut out and used to measure those of the salamanders. Measurements of snout–vent length (SVL) were made from the tip of the snout to the posterior angle of the vent. The specimens were preserved in 10% formalin and later dissected. Data were recorded on the appearance, size, and number of follicles in the ovaries of females, and on the number of testis lobes and condition of the vasa deferentia in males.

Over 2000 *D. monticola* were collected and measured at Wolf Creek (Bruce, 1989, 1990), but only a small proportion were dissected. Most specimens were measured and released. All of the specimens were collected by hand in daytime. Measurements were taken on living specimens which had been anesthetized in either ether or Tricaine (MS-222). Specimens were measured for SVL (posterior angle of the vent) to the nearest 0.1 mm with vernier calipers.

After determining the size at maturation for both sexes by dissecting individuals over a wide range of body sizes, RCB henceforth selected specimens for dissection from the adult size range on a haphazard basis. The sample should have been unbiased according to sex. It was considered relatively unbiased according to adult size, since the dissections were done over a lengthy period, and a given set of dissections was made without reference to sizes of individuals previously dissected. RCB recorded the condition of the oviducts and ovaries and the number of follicles in females, and the number of testis lobes and condition of the vasa deferentia in males.

Statistical tests were run on a Macintosh II computer using either SYSTAT or MYSTAT.

#### RESULTS

*Juveniles.*—The Coweeta samples of juveniles were pooled according to month of collection over the several years of the study. Year to year variation in body-size distribution is probably not pronounced in *D. monticola* in the southern Appalachians (see below). Pooling over an interval longer than a month would have increased sample size, but also would have obscured the separation of age classes by size because of growth effects. Most growth occurs in late spring–early summer in *D. monticola* (Bruce, 1989).

NGH's nighttime sampling procedure was biased against smaller salamanders, particularly first-year individuals; this is evident in comparing the histograms of Coweeta juveniles (Fig. 1) with those of the Wolf Creek samples (Fig. 2), where first-year individuals were apparently underrepresented but nonetheless were present at higher frequencies than at Coweeta. NGH collected eight tiny juveniles (<17 mm) from May through August which could not be accurately measured by his method, and are therefore not plotted on the histograms. Presumably they all represented members of the metamorphosing class of the current year, approximately one year of age. This age class also must have included the small individuals (<22 mm) plotted on the August and September histograms.

For the larger juveniles, the sample sizes at Coweeta were too small to reliably evaluate age

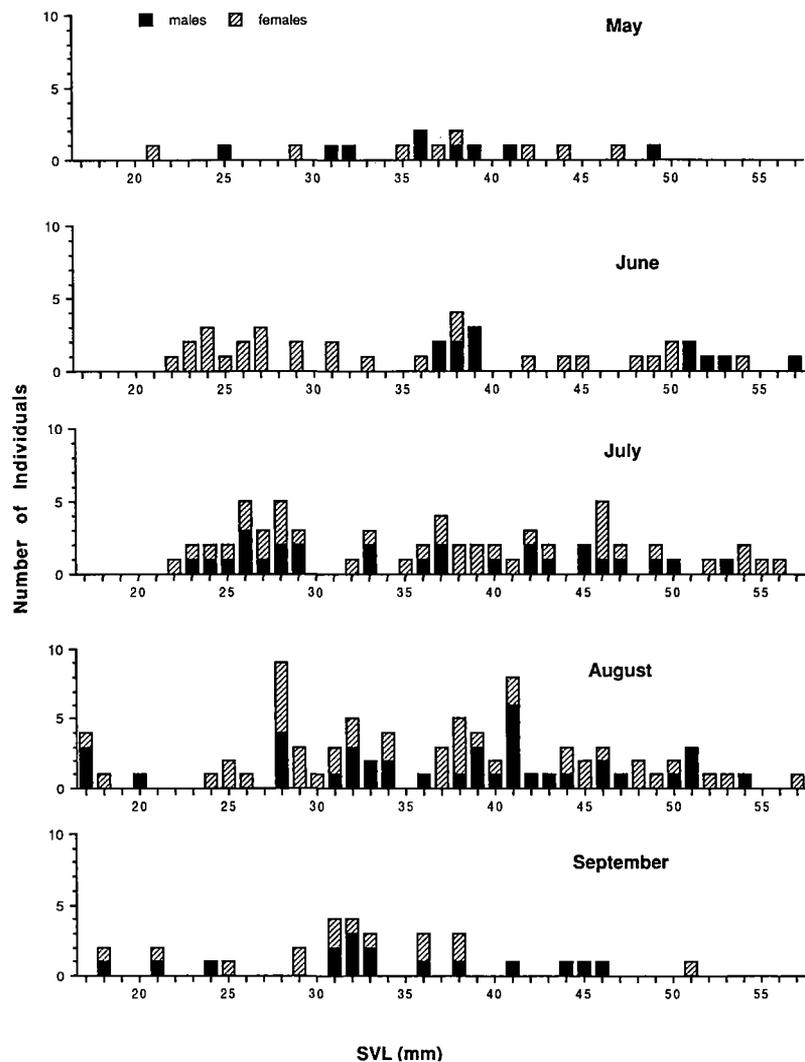


FIG. 1. Distributions of snout-vent lengths of juvenile *Desmognathus monticola* from Coweeta. Pooled data, 1981-1984. Not shown are 8 individuals <17 mm (see explanation in text).

components from the SVL distributions (Fig. 1). Nevertheless, groups of individuals were identified which appeared to correspond for successive samples. The Coweeta samples were deficient in 1-yr olds, but otherwise the salamanders tended to cluster at SVLs close to those of the 2- and 3-yr olds at Wolf Creek (Fig. 2). In particular, the lower ends of the juvenile SVL distributions (which included a few 1-yr olds <22 mm) showed apparent clusters of 2-yr olds at SVLs  $\geq 22$  mm, wherein the mode shifted from <29 mm in June and July to >29 mm in August and September. Gaps were evident in the distributions of the June through August samples, which apparently separated 2-yr juveniles from 3-yr juveniles having a modal SVL near 40 mm.

Bruce (1989, Fig. 3) provided a histogram for *D. monticola* at Wolf Creek in late July-early August which was based on pooled 1986 and 1987 samples. If these data are separated by year, the definitive juvenile components (individuals <46 mm SVL) sort into three size classes (Fig. 2). There were also larger juveniles at Wolf Creek which overlapped in size with adults. These cannot be included in the histograms because only a small proportion of individuals were examined by dissection and thereby correctly identified as immature or mature. Also included in Fig. 2 is a histogram of SVLs of Coweeta juveniles, regrouped according to the same late July-early August sampling period as at Wolf Creek. Another useful comparison is with the SVL distribution of *D. monticola* at Wolf Creek

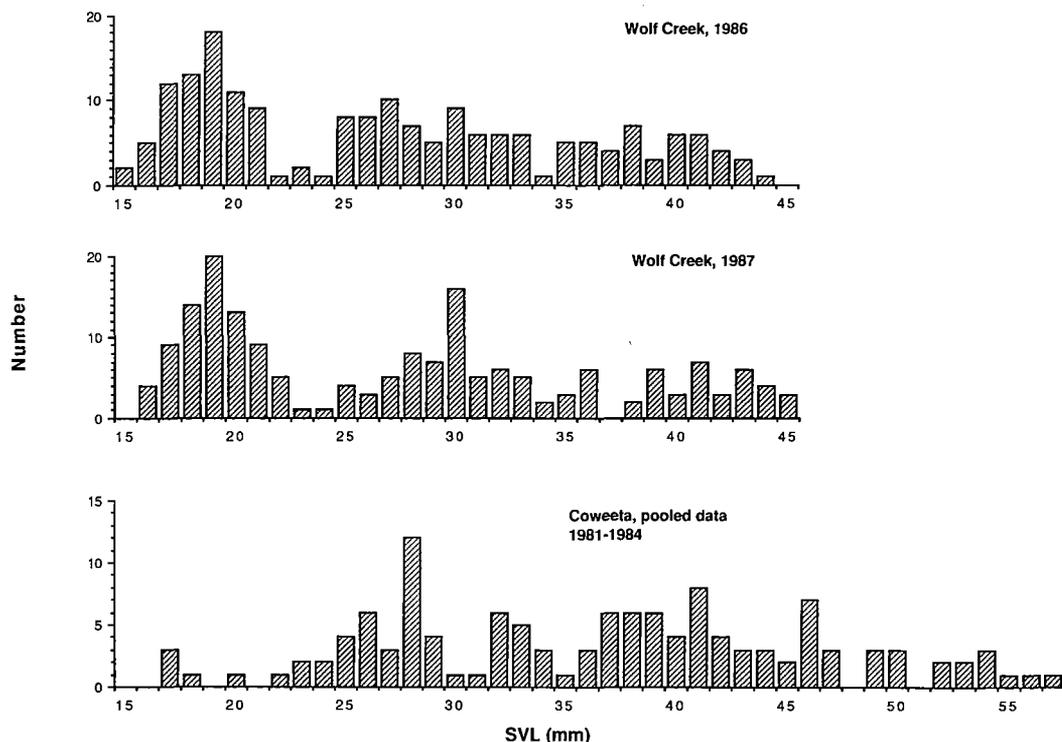


FIG. 2. Distributions of snout-vent lengths of juvenile *Desmognathus monticola* taken in late July-early August at Wolf Creek and Coweeta. The Wolf Creek histograms were obtained by subdividing the histogram of Fig. 3 in Bruce (1989) according to year of collection, and truncating the derived histograms at 45 mm to exclude adults.

in late July-early August 1988 (Bruce, 1990, Fig. 1). The Wolf Creek comparisons support the contention that annual variation in body-size distribution, which reflects variation in juvenile growth, is not pronounced in *D. monticola*. Modal SVLs of the three juvenile size classes were in the ranges 16-19, 27-30, and 38-41 mm over the three years. The Coweeta sample of juveniles for the same period of the summer showed an apparent peak at 17 mm, and additional peaks at 28 and 41 mm. This sample also included larger juveniles (>45 mm) for which no direct comparison was possible with the Wolf Creek data. The important point is that the body-size limits of the 1st, 2nd, and 3rd yr juvenile age classes, insofar as they can be resolved, were quite similar at Coweeta and Wolf Creek. Thus, there is no suggestion that juvenile growth rates were different in the two populations.

However, there was a difference at the upper end of the juvenile SVL distributions. Maximum sizes of immatures at Wolf Creek were 48 mm in males and 52 mm in females (Bruce, 1989). At Coweeta, juveniles of both sexes exceeded these limits, i.e., 14 males (13% of all juvenile males) and 7 females (5.3% of all juvenile females). The maximum size of juveniles

was the same (57 mm) for both sexes at Coweeta. At Wolf Creek, the overlap in sizes at the transition from immature to mature was not more than 2 mm (46-48 mm) for males, and none (52 vs. 53 mm) for females. At Coweeta, the overlap for females was from 52 to 57 mm, with 9 immature and 7 mature specimens; for males, the overlap was from 48 to 57 mm, with 14 immatures and 10 matures. These observations cannot be related to any bias caused by different collecting methods, and are best interpreted as evidence that at Wolf Creek all individuals of the same sex become mature at the same age, whereas at Coweeta age at maturity varies by at least a year for both sexes. We have already presented evidence that early growth is alike in the two areas. Therefore, the obvious interpretation is that maturity is delayed by at least a year for more than half of the Coweeta population.

*Adult Body Size Variation.*—Maximum SVL of males was 80 mm at Coweeta and 72 mm at Wolf Creek (Fig. 3). Thirty-three percent (25/76) of the Coweeta sample of mature males were larger than the largest Wolf Creek male. The SVL data on males were sorted according to testis lobe categories. Because of the decrease in vari-

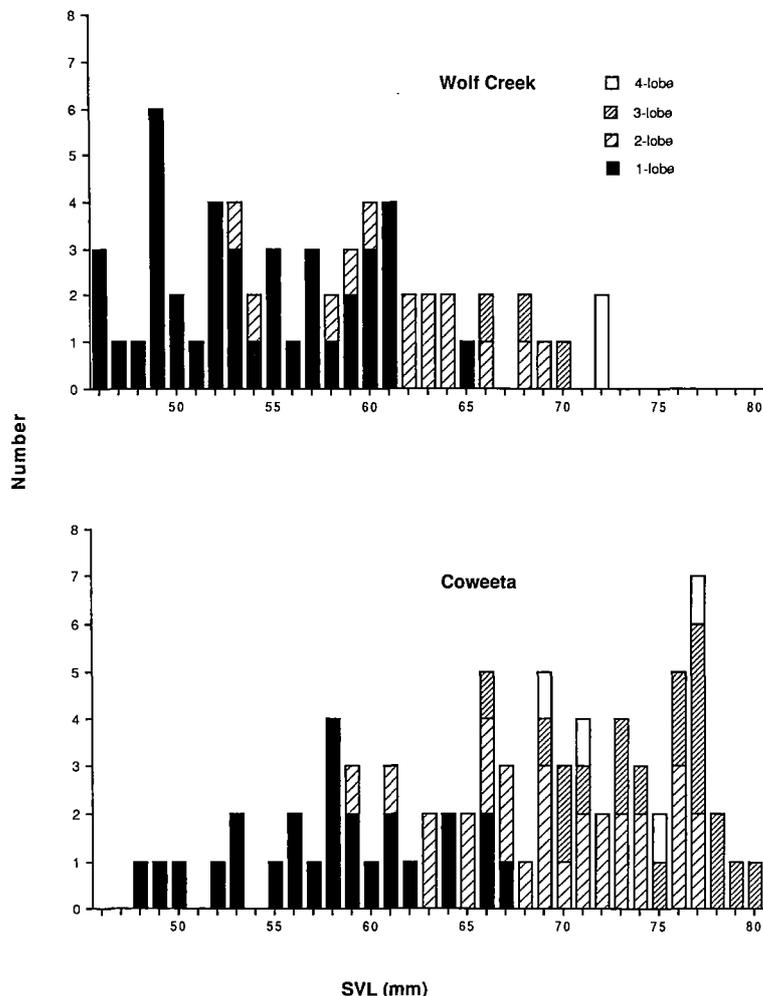


FIG. 3. Distributions of snout-vent lengths of mature males of *Desmognathus monticola*, sorted according to number of testis lobes.

ance of SVL with increase in testis lobe number, the differences in SVL were evaluated by separate ANOVAs for each testis lobe category. There was a significant interpopulational difference in SVL for all but one of the comparisons (Table 1). The larger size of 1-lobed males at Coweeta versus Wolf Creek reflected the larger size at maturity in the former population; as noted earlier, this was apparently an effect of delayed maturity at Coweeta. The magnitude of the difference in average SVL between males of the two populations increased sharply between the 1- and 2-lobed categories. This trend was reversed for the difference between the 2- and 3-lobed males, though the sample size of the latter was small at Wolf Creek. Because of the small number of males with four testis lobes, this last comparison was not reliable. However,

the mean SVLs of the pooled data for 3- and 4-lobed males differed by 4.7 mm, which was only slightly greater than the 4.1 mm difference between 1-lobed males. These comparisons suggested that growth increments for the average spans (2-yr) represented by the testis lobe categories were slightly higher at Coweeta. Thus differences in growth rate may have contributed to the larger sizes attained by Coweeta males over those at Wolf Creek. However, most of the difference probably stemmed from the greater age and size at maturation in the former population.

A comparison of SVLs of dissected females identified as mature revealed differences similar to those for males (Fig. 4). Average SVL of mature females at Wolf Creek ( $N = 43$ ,  $\bar{x} = 58.7$  mm,  $SD = 3.22$ ) was less than at Coweeta ( $N =$

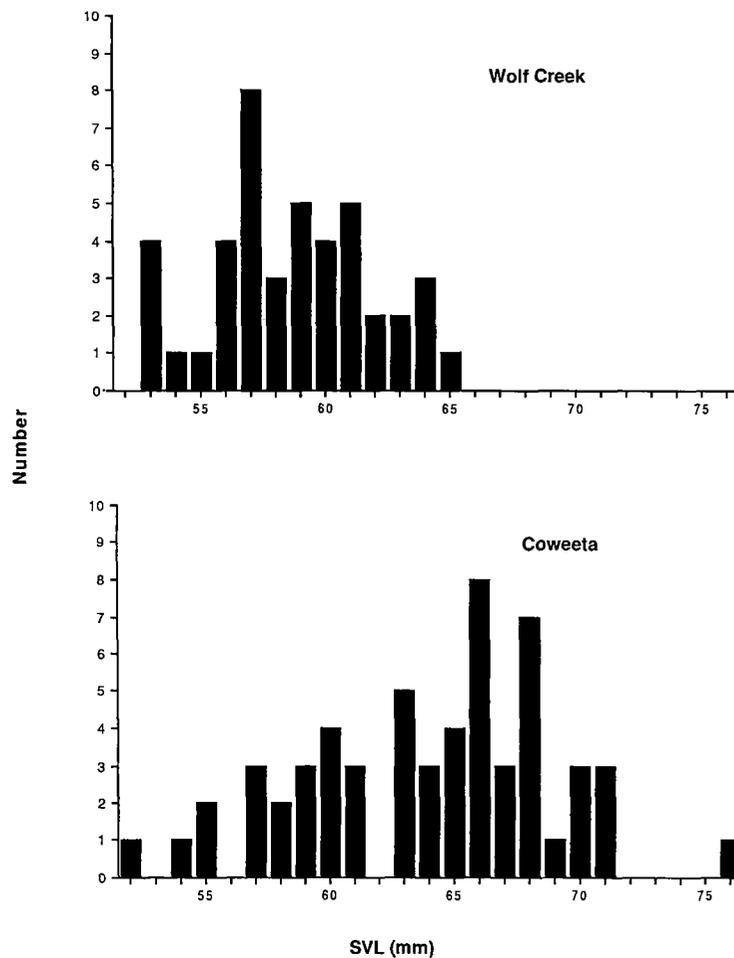
TABLE 1. Comparison of body size in mature males of *Desmognathus monticola*.

Testis lobe category	Wolf Creek			Coweeta			ANOVA		
	N	SVL (mm)		N	SVL (mm)		F	df	P
		$\bar{x}$	SD		$\bar{x}$	SD			
1	40	53.9	5.09	25	58.0	5.28	9.69	1,63	0.003
2	14	61.8	4.68	28	69.6	4.98	23.96	1,40	<0.001
3	3	68.0	2.00	19	74.5	3.84	8.09	1,20	0.01
4	2	72.0	0	4	73.0	3.65	0.13	1,4	0.733
3 and 4	5	69.6	2.61	23	74.3	3.77	6.83	1,26	0.015

57,  $\bar{x}$  = 63.9 mm, SD = 4.99). Although minimum sizes were similar, 26 of 57 (46%) Coweeta females exceeded the maximum SVL observed at Wolf Creek. The largest female at Coweeta was 76 mm, though only this single individual exceeded 71 mm. The difference between populations in the variance of SVL of females was highly significant ( $F = 2.4$ ,  $df = 57, 43$ ,  $P =$

0.002). However, in each population the variance in female SVL was much less than that of mature males.

Based on SVLs of both immature and mature individuals, females at Coweeta attained maturity at 52–57 mm, whereas at Wolf Creek they matured at about 53 mm. There was a much higher proportion of mature females in the 52–

FIG. 4. Distributions of snout-vent lengths of mature females of *Desmognathus monticola*.

57 mm range at Wolf Creek (18/43 = 42%) than at Coweeta (7/57 = 12%). Not shown are the data on immature females at Wolf Creek. Forty-two such individuals ranging from 40 to 52 mm were examined by dissection. Twelve of these varied from 50 to 52 mm, and all had tiny, translucent, non-yolky follicles, and straight, narrow oviducts. All larger females showed some degree of vitellogenesis. Thus we considered 53 mm to be a reliable estimate of size at maturation of females at Wolf Creek.

We have pointed out above the difference in the proportion of small salamanders imposed by the time of day when the collections were made, night collection on the surface being deficient in these individuals. It is also possible that the largest specimens are more easily captured at night, and if that implied bias is great enough, no biological explanation of the differences between the two areas is necessary. Fortunately, during the first year of NGH's experiment at Coweeta removals were carried out during both night and day searches of the plots. The day-time collections, although constituting a smaller sample than is desirable, provide a direct comparison with the Wolf Creek data.

Of a total of 49 specimens 26 (0.53) were within the size range of the two youngest juvenile age classes (above, and Bruce, 1989). In the Wolf Creek spring and summer data, these constituted 509 (0.614) of a collection of 829 specimens. Thus, the younger age classes were higher in proportion at Wolf Creek. Animals in the adult size class at Coweeta ( $\geq 48$  mm SVL) made up a greater part of the sample (13 or 0.26) than they did in the Wolf Creek samples, in which they constituted only 142 of 829, or 0.17. Thus, the larger size of Coweeta *D. monticola* probably was not due to their having been collected mostly at night.

*Male Survivorship.*—It is possible also that survivorship differences accounted for some of the observed differences in body size. Even if growth rates are the same, higher survivorship will yield a greater mean body size. We thought that an evaluation of the frequencies of testis lobe categories might shed light on this question. Although there was an apparent bias in the Coweeta data, where there were fewer 1-lobed than 2-lobed males (N columns of Table 1), there was a negative correlation between number of individuals and number of testis lobes in both data sets. The proportion of males with 3 and 4 lobes was significantly greater at Coweeta than at Wolf Creek ( $\chi^2 = 8.31$ , 1 df, with Yates' correction). The relationship between number of lobes and age is surely settled in a qualitative way, and the data establish the greater proportion of old males at Coweeta, and hence the higher survival after maturity there.

*Reproduction and Fecundity in Females.*—In both populations oviposition is probably concentrated in July, with hatching following in August (or later). RCB has observed egg clutches in mid-July (Bruce, 1990) and a cluster of hatching larvae in late August (Bruce, 1989). Although clutches were not found at Coweeta, NGH found that in 8 of 28 mature females collected in May and June, the maximum follicle diameters were 3.2–4.3 mm, with the remaining females having follicles smaller than 3.0 mm. In contrast, from July through September maximum follicle diameters did not exceed 2.8 mm in the 29 mature females examined. Presumably the gravid females had deposited their eggs by July, and were attending them in subterranean nesting sites which NGH did not attempt to sample. Although RCB did not collect at Wolf Creek in May or June, he dissected 16 mature females taken in July and August. Fourteen had yolky follicles ranging from 1.0–2.9 mm. The other two were recently-spent females taken in late July. Both had thick, twisted oviducts and flaccid ovaries. One had no yolked follicles, but the other had three, which were considered residuals. This female was excluded from the size-fecundity analysis.

Mature females taken at both sites in July and August having partially-yolked follicles had obviously not reproduced in the current summer, and were probably scheduled to reproduce next in the following summer. Undoubtedly, some of these females were undergoing vitellogenesis for the first time. It is possible also that females do not reproduce on a strict annual schedule.

We both counted yolky ovarian follicles in mature females. Counts were obtained for 41 individuals at Coweeta and 15 at Wolf Creek (Table 2). Although these counts were used to estimate clutch size, it is likely that not all yolked follicles are deposited, so that realized clutches average fewer eggs than the ovarian counts. At least one Coweeta female may have been recently spent (57 mm SVL with 4 follicles), but it was included in the regression analysis because data on its oviducal condition were not recorded. Its exclusion would not change the outcome of the interpopulational statistical analysis. At both localities there was a tendency for follicle number to increase with SVL, as evaluated by least-squares regression. However, the regression coefficient was not significantly different from zero at Wolf Creek, and was only weakly significant at Coweeta (Table 3). Inasmuch as both variables were subject to error, the least-squares approach is not strictly valid and the results are only approximate. Even though the mean size of gravid females was greater at Coweeta than at Wolf Creek, the av-

TABLE 2. Comparison of body size and follicle number in gravid females of *Desmognathus monticola*.

Locality	N	SVL (mm)		Follicle no.	
		$\bar{x}$	SD	$\bar{x}$	SD
Wolf Creek	15	58.8	3.23	29.3	5.45
Coweeta	41	66.0	3.75	24.2	7.81
		F = 43.04		F = 5.37	
		df = 1,54		df = 1,54	
ANOVA:		P < 0.001		P = 0.024	

erage follicle count was higher in the latter population (Table 2). Thus females at Coweeta produce fewer eggs per unit of body mass than do Wolf Creek females. We do not have reliable data on possible differences in egg size between the two localities. The measurements on follicle size reported herein and RCB's measurements on field clutches (Bruce, 1990) do not suggest any major difference.

#### DISCUSSION

In *Desmognathus monticola* the larger adult body sizes attained at Coweeta versus Wolf Creek appear to be more a consequence of delayed maturation in the former population, as opposed to faster growth. The variation in body size is inversely correlated with clutch size. Adult survival may be higher at Coweeta, based on the male data. If true, these relationships would suggest that the differences between the populations are evolved differences rather than direct environmental effects. Life history theory predicts that high survival and long life expectancy tend to favor delayed breeding and lower reproductive effort (Tinkle, 1969; Hirschfield and Tinkle, 1975; Wittenberger, 1979). The advantages of delaying maturity and limiting reproduction when survival is high reside in the opportunity for additional growth to larger body sizes, thereby allowing some combination of larger clutches, more effective parental care, and higher juvenile survival in subsequent reproductive seasons (Stearns and Crandall, 1981). Such a strategy should be favored if the chance of not surviving is outweighed by increases in reproduction achieved by delay. Within species, it is expected that habitat variation provides a range of survival probabilities under which local life-history adjustments evolve. The limits

to these adjustments are represented by allometric constraints on body size and morphology of the species in question (Calder, 1984).

Relationships between reproductive effort and survival are complex (Michod, 1979), and we lack reliable survival data. However, what was surprising about *D. monticola* was that clutch sizes were actually lower at Coweeta than at Wolf Creek. Even if age-specific reproductive effort was less at Coweeta, absolute clutch sizes might be expected to average higher because of larger adult sizes. However, lifetime reproductive success can be enhanced by lowering age-specific reproductive effort when local survival conditions are favorable, even if there is no tendency for fecundity to increase with body size. In neither population of *D. monticola* was there a strong trend for clutch size to increase with body size, which is contrary to the situation in most salamanders (Salthe, 1969; Salthe and Mecham, 1974), including other species of *Desmognathus* (Tilley, 1968). The latter author found that *D. monticola* was the only one of five species studied in which fecundity did not increase with increasing body size. In our study of this species, we do not know whether the ovarian follicle counts accurately represented clutch volumes because of lack of data on egg-size variation.

We hypothesize that the observed variation in the life-history of *D. monticola* at Coweeta and Wolf Creek stems from underlying variation in survival; i.e., Coweeta is a safer environment than Wolf Creek. The factors contributing to such a difference are largely unknown. Both areas have similar streamside salamander communities, and the predatory species *Gyrinophilus porphyriticus* and *Desmognathus quadramaculatus* are present in both. One major difference in the physical habitat is precipitation; Coweeta is moister, with annual precipitation averaging >200 cm (Dils, 1957), whereas annual precipitation at Wolf Creek averages about 150 cm (unpubl. data, Dept. Earth Sciences, Western Carolina Univ.).

The studies of Keen (1982), Kleeberger (1984, 1985), Southerland (1986a, b), and Colley et al. (1989) suggested that behavior and activity of *D. monticola* are closely tied to the availability of cover objects and to moisture conditions. Southerland (1986b) proposed that restrictions

TABLE 3. Regression of follicle number on snout-vent length in gravid females of *Desmognathus monticola*. In the equation Y = number of yolked follicles and X = SVL in mm.

Population	N	Regression equation	$r^2$	ANOVA: regression coefficient		
				F	df	P
Wolf Creek	15	Y = - 7.617 + 0.628X	0.139	2.102	1,13	0.171
Coweeta	41	Y = -29.458 + 0.814X	0.153	7.026	1,39	0.012

on foraging activity and effectiveness in *D. monticola* are a combined response to desiccation risks, predation from *D. quadramaculatus*, and competition from other congeners. He has observed predation in the field (Southerland, pers. comm.). Hairston's (1986) experiments were not designed to detect an effect of predation of *D. quadramaculatus* on *D. monticola* at Coweeta. It is possible that moisture limitations restrict foraging and expose *D. monticola* to greater predation risks from the larger, more aquatic salamanders, *D. quadramaculatus* and *G. porphyriticus*, as well as from other kinds of predators. This factor might generate variation in survival probabilities between Coweeta and Wolf Creek sufficient to promote differential selection for the observed variation in life-history traits.

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