Larval Development of the Salamanders Pseudotriton montanus and P. ruber

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ABSTRACT: The larval development of Pseudotriton montanus and P. ruber was studied in the Piedmont of western South Carolina. Larvae of both species hatch in winter and metamorphose in summer. The larval period of P. montanus is usually 17 ± 3 months, but may be prolonged for an additional year. That of P. ruber is ordinarily 30 ± 2 months. However, the growth rate of P. montanus is higher than that of P. ruber, such that the two species metamorphose at nearly the same size. It is suggested that the more rapid growth and shorter larval period of P. montanus have evolved in response to inherently greater hazards in the lowland environments occupied by this species, in contrast to greater stability and safety in the upland habitats of P. ruber. The differences between the species in these life-cycle parameters are considered additional evidence for more intense r-selection in P. montanus than in P. ruber.

INTRODUCTION

The genus Pseudotriton, a primitive representative of the family Plethodontidae, contains two species of semiaquatic salamanders, P. montanus and P. ruber. Both are restricted to eastern United States where they inhabit springs and associated watercourses as well as surrounding terrestrial environments. Although they are sympatric over a large area, P. montanus has a more southern distribution and shows a greater affinity for lowland habitats than P. ruber (Dunn, 1926; Conant, 1958). Within the zone of sympatry local populations may show either total microsympathy or nearly complete habitat exclusion (Bruce, 1968). The life cycles of both species feature lengthy phases of larval development, and the larvae are morphologically generalized and similar to one another. The larval period of P. ruber is about 2.5 years in the southern Appalachians (Gordon, 1966; Bruce, 1972a), and may be longer in the northern part of the range (Dunn, 1915; Bishop, 1925, 1941). That of P. montanus is less well-known, but observations by Netting and Goin (1942), Brimley (1944), Wood (1946) and Goin (1947) suggest an extensive larval period, perhaps similar to that of P. ruber. These and other reports (Brimley, 1923; Fowler, 1946) indicate that in both species, over large sections of their ranges, oviposition, embryonic development and hatching occur in autumn and winter. However, comparative studies of the larval biology of the two species have not been made. It is the intent of this report to provide information on larval development for sympatric populations of P. montanus and P. ruber and to consider the evolutionary significance of the findings in view of other features of the life cycles of these salamanders.
MATERIALS AND METHODS

Samples of larval and recently metamorphosed *Pseudotriton* were obtained at two localities in the Piedmont of western South Carolina between August 1962 and November 1972. Serial collections were made for both species in 1966-67, and supplementary samples were taken in several other years. The total sample included 558 *P. montanus* and 514 *P. ruber*.

Searches were made in springs, small streams and swampy pools and ponds. Collecting was done by hand or, more often, by means of a fine-mesh dip net. The usual procedure was to lift mud and decaying vegetation from the stream bed onto an adjacent sloping bank, and to search this material for larvae. Metamorphosed salamanders were ordinarily found by raking litter along the margins of the watercourses. Most specimens were preserved within a few hours after collection. They were killed by immersion in either 50% ethyl alcohol or a chloretone solution, and were then hardened in 5% formalin. Measurements of snout-vent length (SVL), made from the tip of the snout to the anterior edge of the cloacal slit and recorded to the nearest millimeter, were taken after the salamanders had been in formalin for at least 24 hr.

Some samples were taken in a single day; for others the collecting period extended to 3 weeks. For each sample a length-frequency histogram was constructed, and an attempt was made to identify age classes from the distribution of snout-vent lengths. Because of the small sample sizes, no attempt was made to resolve overlapping polymodal distributions into their components such that age-specific means and variances of snout-vent length could be estimated. However, discrete size groups were present in many samples, and for each such group, apparently homogeneous and inclusive for a particular age class, the mean and variance of snout-vent length were calculated directly. These data allowed some intra- and interspecific comparisons of mean snout-vent lengths of corresponding age classes. All of the t values given later in this paper for such comparisons are for pairs of samples showing homogeneity of variance. A 5% significance level was used in evaluating differences in means and variances.

This study considered three phases of the life cycle: larvae, metamorphosing larvae and recently metamorphosed juveniles. The sequence of events in metamorphosis was similar in both species; obvious changes included development of eyelids and elevation of eyeballs, loss of labial folds, assumption of juvenile pigmentation, loss of caudal fin, attachment of gular fold to throat, loss of external gills and closure of gill slits. Metamorphosis was considered under way if the eyelids had formed and the labial folds showed reduction, and was designated complete if the gills had been resorbed and the gill slits had closed. Evidence of recent metamorphosis included small body size, presence of gill scars and retention of pigmentation characters of metamorphosing larvae. Such individuals had presumably transformed in the year in which they were collected, and, based on the
collection data of metamorphosing larvae, most were probably not more than several weeks beyond metamorphosis.

All of the specimens have been deposited in the vertebrate collection of the Department of Zoology, Duke University.

**Study Areas and Habitats**

The two study areas were located 6 km apart in the upper Piedmont of western South Carolina. One area, designated Newry, was 1 km NW of the town of that name, near the confluence of Cane Creek and Little River, in Oconee Co. This site has since been destroyed by the impoundment of Little River, and now lies beneath the waters of Lake Keowee. The second study area, known as Clemson Forest, was within a research forest owned by Clemson University, about 7 km N of Clemson in Pickens Co. Elevations at both areas were between 200 and 275 m.

At Newry, *P. montanus* was found along a small tributary of Cane Creek. Over most of its 0.5 km course this muddy stream, designated stream B, meandered sluggishly through bottomland deciduous forest, to enter a swampy, shallow pond of about 1.5 ha within the floodplain of Cane Creek. However, the headwater zone of stream B lay in a narrow ravine in upland deciduous forest, and the stream flowed for 75 m along a moderate gradient over a sandy bottom bedded with rock and gravel before entering the bottomland of the lower part of the drainage. Several springs arose at the bases of hillsides bordering the floodplain of the stream and its swampy terminus, *Pseudotriton montanus*, found throughout this drainage, was especially abundant in the swamp, but was also taken in the uppermost headwater springs. Other aquatic plethodontids found along the entire course of this stream were *Eurycea bistineata* and *Desmognathus fuscus*. *Eurycea longicauda guttolineata* was common in the lower part of the drainage, whereas *Gyrinophilus porphyriticus* was observed only in the headwater zone.

*Pseudotriton ruber* was not found in stream B, but did occur in an adjacent drainage (stream A) which discharged into Cane Creek about 100 m downstream from the entry of stream B. Although the headwaters of the two streams were less than 1 km apart, stream A had an entirely different character than stream B. The former, over most of its 1.25 km course, flowed along a moderate to steep gradient through a narrow ravine in upland deciduous forest. Numerous springs lay along its course, and these contained populations of *P. ruber* as well as those of *G. porphyriticus*, *E. bistineata*, *D. fuscus*, *D. monticola* and *D. quadramaculatus*. Neither *P. montanus* nor *E. longicauda guttolineata* were ever observed in the stream A drainage. Thus at Newry, in adjacent drainages within an area of less than 1 km², two assemblages of aquatic plethodontid salamanders were recognized: an upland group of *P. ruber*, *G. porphyriticus*, *D. monticola* and *D. quadramaculatus*; and a lowland group of *P. montanus* and *E. longicauda guttolineata*. The ubiquitous *E. bistineata* and *D. fuscus*
were common to both, and the upland *G. porphyriticus* barely entered the habitat of the lowland assemblage in the headwaters of stream B.

At Clemson Forest, *P. montanus* occurred in a swampy bottomland along Sixmile Creek at the northern end of Lake Issaqueena. The site lay within a mixed forest of pine and bottomland deciduous species. The habitat was a muddy slough, about 60 m in length by 1-2 m in width; the lower end of the slough opened into a shallow swamp of approximately 1 ha. Maximum water depths were ordinarily 10-15 cm; however, most of the habitat was dry in late summer in both 1970 and 1972. The only other aquatic plethodontid commonly encountered here was *D. fuscus*; an occasional individual of *E. longicauda guttolineata* was seen, and a few larvae of *P. ruber* and *E. bislineata* were observed in the slough but not in the swamp.

Numerous other streams draining into Lake Issaqueena, within 2 km of the Sixmile Creek bottomland, lacked *P. montanus* but contained *P. ruber* and the other members of the upland assemblage of plethodontids. These streams, flowing through ravines in upland deciduous forest, were similar to stream A at Newry. Thus, although the local distributions of aquatic plethodontids were similar at Newry and Clemson Forest, habitat exclusion in *Pseudotriton* was less complete at the latter locality, with *P. ruber* entering the bottomland dominated by *P. montanus*, but with no penetration of the latter into the upland habitats occupied by *P. ruber*.

**Larval Development of Pseudotriton montanus**

The most definitive information on the larval development of this species was obtained from series of collections made at both study areas in 1966-67 (Figs. 1, 2). The smallest larvae were taken in early March in both series; in each sample they formed a discrete size group within a narrow range of snout-vent lengths ($\bar{x} = 13.0$ mm). The hatchlings were apparently underrepresented in the March samples, accounting for 58% and 38% of the larvae at Clemson Forest and Newry, respectively. These low frequencies may reflect biased sampling in that tiny larvae were harder to detect in the debris of the dip-net samples; however, they may also indicate that in March hatching had not been completed for the current year. In the hatching larvae the mouth, eyes and limbs were functional for independent life; yolk was present in the gut but produced no pronounced distension. They were larger and more advanced morphologically than the hatchlings described by Goin (1947). It seemed likely that these larvae had hatched between several days and several weeks prior to collection, such that the hatching period might have extended from January into March. For convenience, February was set as the median month of hatching in assigning ages to larvae.

Egg clutches of *P. montanus* could not be located. Presumably the nesting sites are water-filled channels within the banks of streams and pools. Since females of *P. montanus* produce large, yolky eggs which are brooded in the winter, it is probable that the species has a
lengthy incubation period, perhaps similar to or longer than the 2-3-month period suggested by Bishop (1941) for the related *P. ruber* in New York. This would place egg laying in autumn for *P. montanus* in western South Carolina. Such an estimate is supported by my observations of adult females, in which vitellogenesis was in progress in the summer, such that by mid-September most females, having ovarian eggs enlarged to 2.0-2.8 mm in diam, were obviously nearing the time of oviposition. Other workers have reported autumn and winter egg clutches in widely separated populations of this species (Brimley, 1923, 1944; Fowler, 1946; Goin, 1947).

In addition to the 1-month larvae, each March sample of 1967 also contained larger larvae which, on the basis of these samples alone, could be considered a homogeneous class of 13-month individuals. Similarly, the size distributions in spring and summer at both

![Graphs showing length-frequency histograms for *Pseudotriton montanus* from Newry between 14 May 1966 and 11 March 1967. Symbols used: light squares = larvae, squares with crosses = metamorphosing larvae, dark squares = recently metamorphosed individuals.](image-url)
localities were essentially bimodal. Although the late winter through summer series did not represent chronological sequences, the size distributions indicated considerable growth for younger but not older larvae in this period at both localities. Juveniles were recruited from the larger larvae via metamorphosis in the summer of 1966. In addition, at Newry, two metamorphosing larvae (36, 37 mm SVL) were collected on 10 July 1963, and 35 recently metamorphosed individuals (37-47 mm SVL, \( x = 41.9 \) mm) were taken between 10 July and 4 September in 1962, 1963, and 1965. At Clemson Forest nine recently metamorphosed individuals (36-46 mm SVL, \( x = 40.6 \) mm) were collected from 25 July through 13 September in each summer from 1968 through 1970, but such individuals were not taken in several searches made in those years from 11 April through 21 July. However, in 1972 a metamorphosing larva (40 mm SVL) and a recently metamorphosed juvenile (45 mm SVL) were collected at this locality in May. These data indicated a potentially lengthy period of metamorphosis in the warmer months from mid-May to early September, perhaps ordinarily concentrated in July and August. July was set as the median month for termination of the larval period in estimates of the duration of larval life.

Apparently not all of the larger larvae in the 1966 samples were scheduled to metamorphose in the summer of that year. For example, at Newry, metamorphosing larvae were collected in July but not in August, although the latter sample contained a discrete group of large larvae within a narrow range of snout-vent lengths. Whereas recently

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![Graph](image-url)

**Fig. 2.**—Length-frequency histograms for *Pseudotriton montanus* taken from Clemson Forest between 29 August 1966 and 7 May 1967. Symbols as in Figure 1
metamorphosed juveniles were not taken in August 1966 at Newry, they were collected in August in other years, and their absence in 1966 was considered a sampling error; i.e., because of time limitation the sampling effort was expended on larvae, using a different collecting technique than employed for metamorphosed individuals. Although two size classes, presumably representing 6- and 18-month larvae, could be recognized on the August histogram, the older larvae fell within a much narrower range of snout-vent lengths than expected for a representative sample of 18-month larvae; moreover, their frequency was low (11%). These data suggested that the larger members of this age class had undergone metamorphosis in July at 17 months beyond hatching, with the remainder destined to spend an additional year in the larval phase and metamorphose the next summer at 29 months. In November at Newry, the two age classes, now 9 and 21 months beyond hatching, showed a distribution of snout-vent lengths in which discrete size groups could not be recognized. It was from this mixed age class, represented by 13- and 25-month larvae in the March 1967 sample, that the metamorphosing class of next summer would come. By this interpretation the size class of large larvae in the May-June sample of 1966 may have contained both 16- and 28-month larvae, with the category of metamorphosing and recently metamorphosed individuals in the July sample of that year probably including all of the 29-month plus many of the 17-month individuals.

A similar interpretation was applied to the Clemson Forest data of 1966-67. Although a metamorphosing larva was taken on 29 August 1966, the other large larvae from the late summer sample showed no evidence of entry into metamorphosis, and probably would have delayed metamorphosis until the next summer. The two largest larvae (39, 41 mm SVL) in the November 1966 sample may have represented 21-month individuals in this category. The 1966-67 size distributions suggested that growth rates at Clemson Forest were less than at Newry, although evaluation of such a difference was difficult because of uncertainty in identifying homogeneous yet inclusive age groups in pairs of samples taken on nearly the same dates at the two localities. However, in one comparison, between well-defined classes of young larvae, the mean SVL in the 5-16 August sample from Newry (x = 25.8 mm) was greater than that in the 29 August-1 September sample from Clemson Forest (x = 22.7 mm); the difference was highly significant (t = 4.13, P90<0.001).

Other collections of larval P. montanus were made at Clemson Forest in 1970 and 1972. The size distributions in small samples (n = 19) taken in March, April and June of 1970, although inadequate in themselves, conformed to the size data of the earlier samples (i.e., growth within the discrete class of young larvae was similar in 1970 and 1967, whereas the few large larvae in the 1970 samples fell within the size range of older larvae taken in late winter and spring of 1967).
Of greater interest were the two late summer samples of 1972 from Clemson Forest (Fig. 3). The larger, taken between 10-19 August, showed a unimodal distribution of snout-vent lengths with a variance similar to that of the youngest age class in the sample of 29 August-1 September 1966 from this locality ($F = 1.097, P_{20, 103} > 0.2$). The mean SVL for this mid-August sample of 1972 ($x = 27.5$ mm) was greater than that of the youngest larvae in the corresponding sample of 1966 ($x = 22.7$ mm), and the difference was highly significant ($t = 8.47, P_{123} < 0.001$). Thus the sample of August 1972 apparently contained only 6-month larvae; the large size of the sample ($n = 104$) suggested that if older larvae were present in the population, their frequency must have been extremely low. Furthermore, the small mid-September sample of 1972 also contained just one apparent age class (7-month).

The large body sizes of 1st-year larvae in 1972, and the apparent absence of older larvae in the population in late summer of that year, suggested that growth rates of larval *P. montanus* were higher at Clemson Forest in 1972 than in 1966. This resulted in early metamorphosis of not only any 3rd-year holdovers, but of all the 2nd-year larvae as well. Metamorphosis was recorded at Clemson Forest in May 1972, the earliest record over the entire 10-year study period. Thus annual variation in the mean larval growth rate is expressed by varia-

![Length-frequency histograms for *Pseudotriton montanus* taken from Clemson Forest in 1972. Symbols as in Figure 1](image-url)

Fig. 3.—Length-frequency histograms for *Pseudotriton montanus* taken from Clemson Forest in 1972. Symbols as in Figure 1
tion in the frequency of metamorphosis in the 2nd summer, after a larval period of 17±3 months. Perhaps no more than a small fraction of the population ordinarily prolongs the larval period into the 3rd summer, with metamorphosis thereby occurring at 29±3 months after hatching, and there is no evidence that these populations extend the larval phase into the 4th year.

LARVAL DEVELOPMENT OF PSEUDOTRITON RUBER

The five samples taken at Clemson Forest in 1966-67 (Fig. 4) provided the most comprehensive data on the larval period of this species. Because of the small sample sizes, age classes were not always clearly delineated in the length-frequency distributions; nevertheless, the correspondence in the distributions of successive samples gave an adequate picture of larval development of this population, similar to that previously described for nearby Blue Ridge populations of the species (Bruce, 1972a).

Although egg clutches of *P. ruber* were not found, numerous adult females taken in August contained ovarian eggs enlarged to 3.0-4.0 mm in diam, and would probably have oviposited in early autumn. Thus a 2-3-month incubation period, as estimated for this species in

![Graphs showing length-frequency histograms for Pseudotriton ruber](image.png)

Fig. 4.—Length-frequency histograms for *Pseudotriton ruber* taken from Clemson Forest between 24 July 1966 and 7 May 1967. Symbols as in Figure 1
New York (Bishop, 1941), would place hatching in late autumn or early winter. However, hatchlings were not present in the collections of late November and early December of 1966; the smallest larvae were taken in the sample of 1 March 1967. As these were slightly larger than Blue Ridge larvae taken in February in the study noted above, they were probably at least several weeks beyond hatching; for convenience, ages of larvae have been assigned from a January hatching date.

In addition to the 2-month larvae, the March sample contained two size groups of larger individuals, presumably representing 14- and 26-month larvae. In May, the youngest larvae, now 4 months, formed a discrete size class, but the older groups of 16- and 28-month larvae could not be differentiated on the histogram. This may have been a consequence of the small numbers of older larvae, but may also have reflected decreased growth of the oldest larvae during the several months preceding metamorphosis. Such overlap was evident in the July sample of 1966, in which metamorphosis was under way or completed among the larger individuals in the size group containing both 18- and 30-month larvae. In August of that year some metamorphosis was still in progress, but two size groups of nonmetamorphosing larvae were present. By November and December of 1966 the more rapid growth of the younger larvae in the autumn months had resulted in a broad overlap in size of these two age classes, now 11 and 23 months beyond hatching.

In small samples from other years, metamorphosing larvae were taken from June through August. Assuming a December-February hatching period, it seemed likely that most metamorphosing larvae and just-metamorphosed juveniles were in their 3rd summer of life, having completed a larval period of 30±2 months. However, as some larvae may reach metamorphic size in their 2nd summer, it is possible that such individuals metamorphose after a larval period of only 16-20 months. In contrast, the 52-mm and 48-mm larvae taken in August and November, respectively, may have been individuals which had failed to metamorphose at the usual age.

A single sample of larval *P. ruber*, taken in July 1966, was collected at Newry. Three size groups, representing 6-, 18- and 30-month larvae, were present, with metamorphosis in progress among the oldest larvae (Fig. 5). The overall distribution of SVL was displaced to the left of that of larvae taken at Clemson Forest in the same month. Although the Newry sample was taken earlier in July, it did not seem likely that the approximate 2-week difference in collecting dates could have accounted for the difference. The youngest (6-month) larvae in both samples formed discrete size groups, and their mean SVL (18.6 mm at Newry, 20.1 mm at Clemson Forest) were significantly different (t = 3.52, P < 0.001). This comparison included all larvae within the ranges 17-24 mm at Clemson Forest and 15-24 mm at Newry. Although the 24-mm larva from the latter locality may have been in the 18-month class, otherwise the two samples were almost certainly
homogeneous for 6-month larvae. Such a comparison was not made for either of the older age classes of the July samples; however, it appeared that the difference found for 6-month larvae was paralleled for the 18-month and perhaps for the 30-month class, suggesting lower growth rates at Newry than at Clemson Forest.

The Clemson Forest samples of 1966-67 contained 13 larvae of *P. ruber* from the bottomland habitat where the samples of *P. montanus* were collected. These larvae of *P. ruber* were not kept separate from the larger samples of this species from the upland habitats, and were included in the size distributions of Figure 4. In the spring of 1970 small collections of larval *Pseudotriton* were taken at both the upland and bottomland sites, and *P. ruber* was more abundant (n = 14) in the mixed *ruber-montanus* sample (n = 33) from the bottomland than in 1966-67. For these samples, taken in March, April and June, the larvae of *P. ruber* from upland (n = 33) and bottomland (n = 14) habitats were kept separate. The size distributions were concordant with the 1966-67 findings, showing the three size groups expected for this period of the year, but with no indication of more rapid growth among the bottomland larvae.

In 1972 collections of *P. ruber* were made at Clemson Forest in August at both the bottomland and upland habitats, and in November at just the latter sites. The size distributions (Fig. 6) showed that larval growth rates were higher in 1972 than in 1966. For comparison, the mean snout-vent length of the discrete class of small larvae (16-24 mm) taken in August 1966 was compared with that of smaller larvae (19-27 mm) collected in August 1972. Whereas the 1966 subsample was almost certainly both homogeneous and inclusive for

![Fig. 5.—Length-frequency histogram for *Pseudotriton ruber* taken from Newry between 2-16 July 1966. Symbols as in Figure 1](image-url)
7-month larvae, the separation of 7- and 19-month larvae was less certain in 1972. The placement of the upper limit of 7-month individuals at 27 mm probably biased the 1972 subsample by excluding larger 7-month larvae; yet it reduced the chance of inadvertently including older larvae in the younger group, and also reduced the difference in variance between subsamples to nonsignificance (F = 1.540, \( P_{42, 28} > 0.2 \)). Even if the 1972 sample of 7-month larvae was biased through such treatment, the mean SVL of this group (22.9 mm) was still greater than that (20.3 mm) of this age class in the August 1966 sample, and the difference was highly significant (\( t = 5.26, P_{70} < 0.001 \)).

Although the August sample of 1972 from the upland habitats contained metamorphosing and recently metamorphosed individuals within the size range found in other years for these phases, the frequency of nonmetamorphosing larvae of intermediate size (i.e., the 19-month class) was so low that it was uncertain whether the three expected age classes for this time of year were actually represented. Thus, the high growth rate noted for young larvae in 1972, if also characteristic of older larvae, might have resulted in metamorphosis (perhaps largely completed before mid-August) of not only the 3rd-year larvae but of many 2nd-year larvae as well. This possibility was tested by sampling the upland habitats in November 1972. The size distribution was strongly bimodal, showing the presence of 10- and 22-month larvae. Therefore, the sample of the preceding August had undoubtedly contained three age classes, but with an inexplicably poor representation of the intermediate class. As in the August samples of 1966 and 1972, the size distribution for November 1972 was displaced to the right of that of the sample of November-December 1966; however, the irregu-

![Fig. 6.—Length-frequency histograms for *Pseudotriton ruber* taken from Clemson Forest in 1972. Symbols as in Figure 1](image-url)
larity of the latter precluded age-specific comparisons of mean snout-vent lengths of the two autumn samples.

One additional comparison was made between the 1966 and 1972 data on *P. ruber* from Clemson Forest. The mean snout-vent length of metamorphosing and recently metamorphosed individuals taken on 24 July and 29 August 1966 (\(x = 41.8 \text{ mm}\)) was compared with that for these categories in the sample of 19 August 1972 (\(x = 44.8 \text{ mm}\)). Although the difference was not significant at the 5% level, it was sufficient to suggest a greater size at metamorphosis in 1972 (\(t = 1.93, 0.10 > P_{20} > 0.05\)). Since larval growth rates appeared to decrease prior to and during the metamorphic period, the difference in collecting dates probably had a negligible effect on the comparison.

These data showed that within the study area average larval growth rates of *P. ruber* may vary between habitats and, from year to year, within habitats. There is, however, no evidence that such variation has much effect on the duration of larval life or on the timing of metamorphosis. Environmental effects on the mean size at metamorphosis appeared slight in respect to individual variation in growth in a given habitat in a particular year. It is concluded that the usual length of the larval period is 30±2 months in these populations.

Comparison of the Two Species

In western South Carolina both species of *Pseudotriton* have winter hatching and summer metamorphic periods. Although most *P. ruber* metamorphose 1 year later than most *P. montanus*, the growth rate of the latter is higher, such that the two species show a broad overlap in size at metamorphosis. However, because of almost complete habitat exclusion, it is uncertain whether the observed differences in growth rates were of intrinsic or extrinsic origin.

Age-specific comparisons of mean snout-vent lengths could be made for the youngest larvae in the pairs of samples of *P. montanus* and *P. ruber* taken at Clemson Forest in August-September 1966 and in March and May 1967 (Figs. 2, 4). The samples of *P. ruber* were drawn mainly from the upland habitats but contained a few larvae from the Sixmile Creek bottomland where the samples of *P. montanus* were taken. As shown in Table 1, the youngest larvae of *P. ruber* were larger than those of *P. montanus* in March; this could indicate either an earlier hatching date or a larger size at hatching for *P. ruber*, although the former interpretation was followed in assigning ages. By May the youngest larvae of the two species were of similar size, whereas in the August-September samples of the previous year the youngest larvae of *P. montanus* had been larger than those of *P. ruber*. Although these comparisons clearly showed the more rapid growth of *P. montanus* over *P. ruber* in the 1st year of life, the difference may have reflected an environmental effect, *e.g.*, temperature differences between upland and bottomland habitats.

The more interesting comparisons were those between micro-
Table 1.—Comparisons of mean snout-vent lengths of young larvae of *Pseudotriton montanus* and *P. ruber* from Clemson Forest. Based on the data of Figures 2 and 4

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sympatric populations of the two species; however, the high level of habitat exclusion made it difficult to obtain sufficient samples for such analyses. In spring 1970 small collections of both species were taken on the same dates from the bottomland at Clemson Forest; the data for the youngest larvae indicated more rapid growth of *P. montanus*, so that on 14 June the mean size of 4-month *P. montanus* (18.4 mm SVL, n = 7) was greater than that of 5-month *P. ruber* (15.7 mm SVL, n = 3), a significant difference (t = 3.51, P8 < 0.01). In 1972 larvae of both species were collected from this habitat in the same period in August (Figs. 3, 6); the mean size of the few 7-month *P. ruber* (22.7 mm SVL) was less than that of the more numerous 6-month *P. montanus* (27.5 mm SVL), a highly significant difference (t = 5.45, P110 < 0.001). There was no difference between the mean snout-vent lengths of 7-month larvae of *P. ruber* from the bottomland and upland habitats in August 1972 (t = 0.220, P49 > 0.5); however, as noted earlier, the estimated mean of the upland subsample was deliberately biased because of uncertainty in separating 7- and 19-month age classes in the size distribution. These limited observations suggested that the larvae of *P. ruber* have similar growth rates in upland and bottomland habitats, and that the difference in growth rate between the species is of genetic origin. It is conceivable, however, that the low growth rate of *P. ruber* in the bottomland was an effect of interaction with *P. montanus*, with the latter having competitive superiority in such habitats.

A final comparison between the species concerned size at metamorphosis, and was based on the data for all metamorphosing and recently metamorphosed individuals of both species taken at Newry and Clemson Forest during the entire study period. This included snout-vent lengths of 55 *P. montanus* collected between 14 May and 13 September, 1962-72, and of 28 *P. ruber* taken between 14 June and 29 August, 1966-72. More precise comparisons for specific localities in particular years could not be made because of the inadequacy of the samples; nevertheless, the pooling of all available data gave an overall picture of metamorphic size within the total study area. Although there was a broad overlap between the species, the mean for *P. ruber* (42.9 mm SVL) was slightly higher than that for *P. montanus* (41.2 mm SVL), and the difference was just significant at the 5% level (t61 = 2.21). Thus, despite the shorter larval period of *P. montanus*, the more rapid growth of this species results in metamorphosis at an average size very close to that of *P. ruber*.

DISCUSSION

The life cycles of *Pseudotriton montanus* and *P. ruber* are similar in such characteristics as season of hatching, season of metamorphosis and body size at metamorphosis. A striking difference is in the larval growth rate, such that most larvae of *P. montanus* metamorphose in their 2nd summer at nearly the same size as metamorphosing *P. ruber* in their 3rd summer. This does not seem to be an environmental effect,
since in the one habitat where both species occurred there was a difference in growth rate comparable to that of separate populations of the two species. Thus the disparity in larval growth rates presumably has a genetic basis, stemming from differential selective pressures operative within the adaptive zones of northern/upland and southern/lowland representatives of the genus.

Among plethodontid salamanders the predominant evolutionary trend has been toward an increasingly terrestrial mode of life associated with outward radiation from the ancestral environment of Appalachia; a secondary trend, toward abandonment of the post-metamorphic phase through paedogenesis, is associated with adaptation to cave habitats (Wake, 1966; Brandon, 1971). Pseudotriton, retaining primitive morphological features, represents an early stage in plethodontid phylogeny, and both species retain strong ties with aquatic environments. Yet adults often occupy terrestrial habitats, with P. ruber showing less specialization in terrestrial habitat selection than the mud-burrowing P. montanus (Bruce, 1968). Istock (1967) has argued that two-phase life cycles, as found in these and other plethodontids, are inherently unstable because the adaptive rates of change are largely independent for the two phases, thereby generating selection against one of them. The evolution of plethodontids and the phylogenetic position of Pseudotriton can be considered from this viewpoint. Within the family, interspecific morphological variation is greater among post-metamorphic than among pre-metamorphic phases, with the duration of the latter showing marked variation. Therefore, it appears that the acquisition of new adaptations at the adult level, often associated with entry into terrestrial environments, coupled with the evolutionary conservatism of the larval form, has engendered selection against the latter with a consequent shortening of the larval period. This trend is evident in several evolutionary lines of the family, and has led to the abandonment of aquatic reproduction and loss of the free-living larval phase in the most advanced groups of plethodontids (Wake, 1966).

For Pseudotriton, the more rapid growth and shorter larval period of P. montanus versus P. ruber may represent a response by the former to more hazardous and uncertain larval environments and a consequent greater disparity between pre- and post-metamorphic survivorship. Such a response has allowed the species to accelerate development to maturity and reduce the time spent in the larval phase, while retaining ancestral body-size characteristics, especially size at metamorphosis and size at initial reproduction. Although survivorship data are lacking, in this study the larval habitats of P. ruber were less subject to seasonal drying than those of P. montanus. Moreover, differences between the species in age at maturity and fecundity (Bruce, 1968, 1969, and unpubl. data) suggest a more r-selected life cycle for P. montanus than for P. ruber; such a trend toward r-selection is expected for populations subject to high density-independent mortality (Gadgil and Solbrig, 1972).
The reproductive characteristics of *P. montanus* may represent a quantitative extreme among plethodontid salamanders, one that has allowed the species to successfully enter the lowland environments of the southeastern United States while keeping the essential morphological attributes and mode of life of a primitive form. Those of *P. ruber*, a species which has retained an association with the ancestral uplands, are correspondingly less modified from the presumed ancestral condition as, for example, shown by the primitive montane species, *Gyrinophilus porphyriticus* (Bishop, 1941; Bruce, 1972b). Thus, the species of *Pseudotriton* are herein viewed as early representatives of a pattern of radiation in which initial success in a new environment is achieved through a shift from *K*- to *r*-selected parameters of growth, generation time and fecundity. It is expected that this period is followed by one of finer adaptation to the new environment at morphological, physiological and behavioral levels, accompanied by some degree of reversal to a *K*-selected life cycle. It is this second period of adaptation which might include changes in the partitioning of the life cycle between pre- and post-metamorphic phases that are achieved through changes in size at metamorphosis as well as other body-size characteristics. This hypothesis is compatible with that of Istock (1967) for the evolution of two-phase life cycles, as considered within the model proposed by MacArthur and Wilson (1967) for general cycles of colonization.

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References

Brimley, C. S. 1923. The dwarf salamander at Raleigh, N.C. *Copeia*, No. 120:81-83.


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