LIFE-HISTORY PATTERNS OF THE SALAMANDER
GYRINOPHILUS PORPHYRITICUS IN THE
COWEE MOUNTAINS, NORTH CAROLINA

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ABSTRACT: Two forms of the salamander Gyrinophilus porphyriticus inhabit the Cowee Mountains in Jackson, Macon, and Swain counties, North Carolina. A small morph, allied to populations in the adjacent Blue Ridge and Piedmont, occurs in the southeastern part of the Cowees, whereas a large morph, related to populations in the nearby Nantahala Mountains, occupies the northwest. There appears to be neither intergradation nor coexistence between the two where their distributions approach one another at Watauga Gap, about midway along the length of the main Cowee ridge. The pronounced differences in adult body size and fecundity between the 2 Cowee morphs result from a greater time required for attainment of maturity following metamorphosis in the northwestern populations. Such differences among populations in the Cowee and adjacent ranges are thought to represent adaptive responses related to the environmental history of the southern Blue Ridge Province.

The plethodontid salamander Gyrinophilus porphyriticus inhabits the Appalachian Mountains and adjacent areas from southern Canada to central Alabama. All of the nonpaedogenetic members of the genus are now referred to this species (Brandon, 1966, 1967; Conant, 1975). Earlier workers, having inadequate samples of specimens, had designated the populations of the southernmost Blue Ridge Province as either 1 or 2 distinct species, Gyrinophilus danielsi (Blatchley, 1901; Dunn, 1926; Reese, 1950) and Gyrinophilus dunnii (Mittleman and Jopson, 1941; Mittleman, 1942). Brandon (1966) considered both G. danielsi and G. dunnii as subspecies of G. porphyriticus in the southern Blue Ridge; his range map showed a complex pattern of intergradation among these and 2 other subspecies, G. p. porphyriticus and Gyrinophilus porphyriticus danielsi.

In relying on pigmentation as the main criterion for distinguishing subspecies, Brandon overlooked very real and pronounced geographic variation in adult body size among southern Blue Ridge G. porphyriticus. In a previous paper I showed that adult body size in populations occupying the southeastern edge of the Blue Ridge and the nearby Piedmont is considerably less than in those of the Balsam and Nantahala mountains (Bruce, 1972). The size differences and associated differences in age at maturity and fecundity were seen as alternative life-history tactics evolved in response to environmental gradients. Variation in the habitat conditions and abundance of G. porphyriticus provided additional support for the contention that lower elevation, peripheral populations in the Piedmont and Blue Ridge are more r-selected, whereas those at higher elevations in the Nantahala and Balsam mountains are more K-selected.

This report extends the analysis to another mountain range, reinforces the findings of the earlier study, and questions the current taxonomic status of G. porphyriticus in the southern mountains.

STUDY AREAS, MATERIALS, AND METHODS

The Cowee Mountains extend northwestward from the Blue Ridge in Jackson, Macon, and Swain counties, North Carolina (Fig. 1). The southeastern part of the Cowee range is a broad, plateau-like highland; the major peaks are Yellow (1563 m) and Shortoff (1524 m) mountains. The northwestern section is narrower and lower; the highest peak is Cowee Bald (1507 m). A boundary between these 2 divisions can conveniently be set at Watauga Gap, on the divide between Watauga Creek and Sugar Branch of Savannah Creek; at 990 m
Fig. 1.—The Cowee Mountains, North Carolina. The dashed line shows the 914.5 m contour, the dotted line the Blue Ridge Divide, and the dark circle Watauga Gap. The numbers, corresponding to those in the text, show localities at which *Gyrinophilus porphyriticus* was collected.

it is the lowest point along the main Cowee Ridge. The Cowees are surrounded by more massive ranges. The Nantahala Mountains lie to the southwest across the Little Tennessee Valley, and the Great Smoky and Balsam mountains lie to the north and northeast across the Tuckasegee Valley. To the south the main Cowee ridge joins the Blue Ridge at an elevation of 1329 m just north of Cowee Gap.

Samples of *Gyrinophilus porphyriticus* were collected from springs and small headwater streams at the localities listed below. The numbers correspond to those in Fig. 1.

Northwest.—(1–4) Between Leatherman and Blazed Gaps, 1–3 km W of Cowee Bald, Alarka Creek, 1220–1340 m, Swain County. (5) N slope Brushy Fork Mt., Brushy Fork Creek, 1040 m, Jackson County.

Southeast.—(6) Cullowhee Gap, SE of Kirby Knob, Ellijay Creek, 1110 m, Macon County. (7) Between Brown Mt. and Cherry Knob on Cullowhee Mt., Wolf Creek, 975–1160 m, Jackson County. (8) Hamburg Gap, N slope Yellow Mt., Knob Creek, 1340 m, Jackson County. (9) N slopes of Shortoff and Cole Mts., Buck Creek, 1250–1340 m, Macon County.

In the northwestern section a total of
613 larvae and 81 metamorphosed individuals were taken between 1973 and 1975, mainly from several headwater tributaries of Alarka Creek at similar elevations and within 2 km of one another. The salamanders taken at the different sites were similar, and were treated as a sample from a single locality. Most of the larvae were collected in August, December, and April 1973–1974. The metamorphosed individuals were taken on an irregular schedule in every season.

In the southeastern region the majority of specimens came from a series of springs and streams contributing to Wolf Creek on Cullowhee Mountain. As the specimens from the other localities agreed closely in pigmentation, body size, and reproductive characters with those from Wolf Creek, they were pooled with the latter for comparison with the northwestern sample. A total of 471 larvae and 92 metamorphosed salamanders were collected from the southeastern localities from 1966 through 1976. Larvae were taken in every month, and metamorphosed individuals in every month but August.

The salamanders were located in daytime by raking rocks and gravel in the streambed and excavating loose soil and rock in the adjacent bank. The specimens were preserved in 7–8% Formalin within several days after collection. Measurements were made after the salamanders had been in Formalin at least 24 h. The index of body size used in this report is the snout-vent length (SVL), measured to the nearest millimetre from the tip of the snout to the anterior end of the cloacal opening.

The reproductive organs of all metamorphosed individuals were examined by dissection. In females the condition of the ovaries and oviducts was recorded; measurements were taken to the nearest 0.1 mm of the diameter of each oviduct midway along the length of the ovary and of the diameters of several of the larger ovarian oocytes. In males the pigmentation and shape of the testes and vasa deferentia were noted. The presence or absence of spermatozoa in the vas deferens was determined by squash preparations. The spermatogenic cycle was studied from longitudinal sections of testes stained with hematoxylin and eosin. The above procedures allowed recognition of the following reproductive categories:

Females.—In those females considered immature the ovaries were compact, the oocytes were small (<1.2 mm), and the oviducts were straight and thin (0.1–0.5 mm). Mature females were separated into nongravid and gravid categories. In the former the ovaries had a less compact, more flaccid appearance than in immature individuals; oocyte diameters were 0.8–1.9 mm. Such individuals had convoluted oviducts 0.5–1.5 mm in diameter. Gravid females had large, yolked oocytes (>2.0 mm); their oviducts were convoluted and thickened (0.8–1.8 mm). In each gravid female the number of large, yolked oocytes was counted and the total from both ovaries was used as an estimate of the egg complement of the next clutch. The arbitrary distinction between the nongravid and gravid categories of mature females helped insure the reliability of counts of oocytes presumably destined for the next clutch.

Males.—In immature males the testes were narrow, lightly pigmented germ cords, and the vasa deferentia were narrow, straight, and white. In such individuals spermatogenesis was not in progress, and spermatozoa were not seen in the vasa deferentia. Mature males had larger, pigmented testes, and coiled, black vasa deferentia. Mature males having empty vasa deferentia were designated nonbreeding; those having the vasa filled with spermatozoa were considered to be in breeding condition.

The specimens have been placed in the vertebrate collection of the Department of Zoology, Duke University.

Population Structure

At the northwestern study areas on Alarka Creek large numbers of larvae were collected during short periods in August
(n = 220) and December (n = 222) 1973, and in April (n = 166) 1974. With the exception of hatchling larvae (12–13 mm SVL) taken in August, the distributions of snout-vent lengths were continuous within the range 16–71 mm in all 3 samples. No pronounced size groupings were evident in a given sample, nor was there any obvious correspondence among the 3 samples in the size-frequency distributions. Thus, whereas the wide range of body sizes suggested the presence of several year classes of larvae in the population, the lack of discontinuities in the size distributions precluded the identification of age classes and subsequent determination of larval growth rates and the length of the larval period.

Similar results were obtained at the southeastern localities. At Wolf Creek 377 larvae were taken in 5 evenly-spaced collections between December 1973 and July 1975; the range of sizes was 14–64 mm SVL, but the larvae did not sort by size into a consistent pattern that could be related to the population age structure. It therefore appears that in both sections of the Cowees G. porphyriticus has either an extended reproductive season or highly variable growth rates, or both.

At Alarka Creek hatchling larvae were found on 26 August 1973; others were obtained in the laboratory in July and August 1974 from eggs collected at this locality on 13 July 1974. The conditions under which each group was found and the latter group reared are described later. No eggs or hatchlings were found at any of the southeastern Cowee sites.

Only 1 metamorphosing larva (59 mm SVL), taken at Wolf Creek on 9 July 1973, was observed in the southeast. At the northwestern habitats three metamorphosing individuals were collected: in 1973 on 11 and 14 August (70, 65 mm SVL), and in 1974 on 13 July (64 mm). These few records plus the lack of metamorphosing larvae in other seasons suggest that metamorphosis ordinarily occurs in the summer in the Cowee populations of G. porphyriticus. The larger size of metamorphosing individuals in the northwest, as well as the greater maximum larval size in the northwestern versus southeastern populations, indicate either a slightly higher growth rate or a somewhat lengthier larval period in the former.

The remarkable differences between the southeastern and northwestern Cowee populations are illustrated by the size-frequency distributions of metamorphosed individuals in the total samples from the two sections of the mountain range (Fig. 2). Not only was maximum adult size greater by 33 mm in the northwestern than in the southeastern sample, but nearly half the individuals of the former exceeded the maximum size in the latter. The minimal size of metamorphosed individuals was nearly the same in the 2 samples; thus the greater adult size in the northwest was not mainly a consequence of a difference in metamorphic size, even though northwestern larvae probably transform at a slightly larger size than those in the southeast. Rather, the differences in the size distributions can be attributed to the size at which sexual maturity is attained and to the time required for growth to maturity following metamorphosis.

This relationship is especially evident in females. In the southeast only 9 of 52 females were immature, and most of these were within or just outside the larval size range. Immature females were found in every season of the year; thus, if metamorphosis is concentrated in the summer, as suggested above, some southeastern females may not mature until nearly a year after metamorphosis. However, the 2 smallest females (58 mm SVL), both having convoluted oviducts and oocytes enlarged to 1.6–1.7 mm, were unquestionably mature. As both were collected in November, they may have metamorphosed in the previous summer and matured immediately. The presence of other small, mature individuals in the autumn months suggests that southeastern females often undergo rapid development to maturity after metamorphosis. In contrast, in the northwestern
sample a larger proportion (19/37) of the females were immature, there was no size overlap between immature and mature females, and the smallest mature individual was 14 mm larger than the largest larva. These data show that northwestern females remain immature for a longer period than their southeastern counterparts. Presumably this delay of 1st reproduction provides the additional postmetamorphic growth that is responsible for the greater body size of adult females in the northwestern populations.

Among males of either population the proportion of immature individuals was less than in females; in both samples the immature males fell within the larval size range. Thus males generally develop more rapidly than females, and probably mature within the 1st year after metamorphosis in both populations. Yet, as immature males were more prevalent in the northwest (12/44) than in the southeast (2/40), it is likely that a greater tendency for delaying maturity exists among males in the former population.

It can be argued that the interpopulational differences in adult body size are effects of differences in growth rate only rather than age at maturity. However, if the time to maturity following metamorphosis is constant (in a given sex) and just the growth rate varies, then the ratio of immature to mature individuals should be the same in the 2 populations. Chi-square tests of independence do not support this contention; in both sexes the differences between samples in the frequencies of immature and mature individuals are highly significant (Table 1). Similar findings were obtained in the earlier study of G. porphyriticus (Bruce, 1972). Although other factors (e.g., differential mortality rates) could yield similar results, there is no available information on such effects. The simplest explanation of the data is that variation in adult body size in southern Blue Ridge populations of G. porphyriticus is a consequence of differences in age at 1st reproduction.

The pronounced difference in the distributions of snout-vent lengths between the northwestern and southeastern samples obviated the need of a formal significance test of the difference. Within either population there was no significant difference in the overall body-size distributions of males and females; nor did the sex ratio differ from 1:1 in either (Table 2).

**Male Reproductive Cycle**

The course of the male reproductive cycle of G. porphyriticus was studied from longitudinal sections of testes and squash preparations of the vasa deferentia of males collected at different seasons of the year. No differences were found between the cycles of southeastern and northwestern Cowee males, and the following description applies to both.

**Table 1.**—Data and results of chi-square tests of independence of population source and reproductive condition of metamorphosed *Gyrinophilus porphyriticus* in the Cowee Mountains.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Population</th>
<th>Sample size</th>
<th>Chi-square test</th>
</tr>
</thead>
<tbody>
<tr>
<td>♀ ♀</td>
<td>Southeast</td>
<td>9 43</td>
<td>11.6 &lt; .005</td>
</tr>
<tr>
<td></td>
<td>Northwest</td>
<td>19 18</td>
<td></td>
</tr>
<tr>
<td>♂ ♂</td>
<td>Southeast</td>
<td>2 38</td>
<td>7.5 &lt; .01</td>
</tr>
<tr>
<td></td>
<td>Northwest</td>
<td>12 32</td>
<td></td>
</tr>
</tbody>
</table>
Table 2.—Comparisons of distributions of snout-vent lengths of ♀ ♀ and ♂ ♂, and chi-square tests of 1:1 sex ratios of metamorphosed Cyrtophis porphyriticus in the Cowee Mountains, based on the data of Fig. 2. The size distributions were compared by Wilcoxon 2-sample tests (Sokal and Rohlf, 1969).

<table>
<thead>
<tr>
<th>Locality</th>
<th>N</th>
<th>SVL distributions</th>
<th>Sex ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>♀ ♀</td>
<td>♂ ♂</td>
<td>U, t, p</td>
</tr>
<tr>
<td>Northwest</td>
<td>37</td>
<td>44</td>
<td>962.5, 1.409, &gt;.1</td>
</tr>
<tr>
<td>Southeast</td>
<td>52</td>
<td>40</td>
<td>1156.5, 0.920, &gt;.2</td>
</tr>
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As in other plethodontid salamanders, the events of spermatogenesis in G. porphyriticus proceed as a caudo-cephalic wave over the length of the testis. Spermatozoa of a given cycle are 1st generated in late July and August, beginning in the posterior ampullae of the testis. The vasa deferentia are empty at this time. During August and September spermatoeleosis spreads anteriorly; by mid-September spermatozoa are found in ampullae throughout the testis. The posterior ampullae begin evacuation by mid-September, so that the vasa deferentia start filling with spermatozoa at this time, and by October all males have sperm-laden vasa. This condition persists through the winter and spring; the latest date on which spermatozoa were observed in the vasa deferentia was June 9. Proliferation of spermatogonia of the next cycle, beginning posteriorly, is underway before the spermatozoa of the current cycle have left the testis; generally, testes that were examined from males collected from October through mid-December had spermatozoa in the anterior ampullae, with dividing spermatogonia in the partially-evacuated posterior ampullae. By February there may be some spermatozoa left in the anterior-most ampullae, but the emptying of the testis is nearly completed. The anterior ampullae are proliferating spermatogonia, whereas the differentiation of primary spermatoocytes has begun posteriorly. By April and May most of the testis contains primary spermatoocytes, although spermatogonia may still occupy the most anterior regions. The meiotic wave begins in early to mid-July, producing spermatids in the posterior ampullae, and reaches the anterior end of the testis by mid-August.

Inasmuch as spermatozoa are present in the vasa deferentia for nearly 9 months, from late September until early June, G. porphyriticus has a potentially lengthy breeding period. There is no evidence that mating is concentrated at any particular time within this period.

**Female Reproductive Cycle, Fecundity and Oviposition**

The course of the female reproductive cycle of G. porphyriticus was interpreted from data on the reproductive organs of dissected specimens, supplemented by very limited field observations of eggs and hatching larvae. Because there was overlap in body size between immature and mature females at the southeastern localities, and because oocyte sizes of the 2 also overlapped, there was a potential difficulty in distinguishing immature females from those that were mature but nongravid. However, as noted earlier, females were also separated by the condition of the oviducts and compactness of the ovaries. Moreover, the validity of the criteria used to identify the reproductive condition of southeastern females was supported by body-size data; the mean and standard deviation of snout-vent length were very close in nongravid (69.0 ± 5.74 mm, n = 24) and gravid (68.9 ± 5.47 mm, n = 19) mature females, in contrast to the lower values of both statistics in immature females (65.2 ± 2.99 mm, n = 9).

For the southeast, a plot of maximum
oocyte diameter against collection date of mature females showed that while gravid females were taken in each month from October through May, nongravid individuals were also prevalent throughout this period (Fig. 3). Whereas the mature females showed a continuous distribution of maximum oocyte sizes in the autumn, they fell into 2 groups on the basis of egg size in winter and spring, with the largest egg sizes being attained in the latter season. Thus some mature females, in preparation for oviposition, undergo gradual vitellogenesis from autumn through spring, while others retain small oocytes during this period. The slight downward trend in egg size in the latter group from early November to early June may be a consequence of the small sample size. The data suggest that in the southeastern Cowee populations oviposition ordinarily occurs in late spring and summer, but that females do not reproduce on a strictly annual schedule.

At the northwestern localities, where the immature and mature females were completely separated according to body size, the distinction between immature and nongravid, mature individuals was clearer than in the southeast. Only 18 mature females were collected in the northwest, and just 7 of these were gravid. Both nongravid and gravid females were found in every season. The latter were taken in August (2), September (2), December (1), and April (2). Although the 2 April specimens had oocytes enlarged to 3.3 and 3.6 mm, females taken in September and December also had oocytes exceeding 3 mm in diameter. These meager data suggest that northwestern females, like those in the southeast, do not oviposit on a precise annual schedule, and that perhaps egg-laying is less regularly seasonal in the northwest than in the southeast. Yet the discoveries of an egg clutch and a group of hatchling larvae in the field, both in summer, indicate that oviposition is probably concentrated in the warmer months in the northwestern populations. Possibly females retain yolked oocytes in their ovaries for a lengthy period prior to oviposition in the summer.

Counts of yolked oocytes in the ovaries of gravid females ranged from 17 to 60 ($\bar{x} = 34$) in the southeast and from 65 to 101 ($\bar{x} = 82$) in the northwest. The much greater potential clutch size in the latter can be attributed to the larger size of adult females in these populations. Plots of oocyte number against snout-vent length, with both variables transformed to natural logarithms, show this correlation (Fig. 4). Despite the small sample sizes and wide point scatters, the log-log plots show reasonable approximations to straight-line relationships. Regression equations, calculated by Bartlett’s method (Simpson et al., 1960), were fitted to the southeastern sample data and to the pooled data of both the southeastern and northwestern samples. Within the southeastern population it is obvious that the number of yolked oocytes increases with body size. It is likely that a similar relationship exists in the northwest, although the number of
proximately, was buried in loose gravel among percolating water currents ~ 25 cm below the surface of the streambed.

The eggs and female were returned to the laboratory. Five of the eggs, containing embryos in a tailbud stage, were immediately preserved, as was the attending female. The other 19 eggs were placed in a finger bowl in aerated springwater, and maintained at cool room temperatures (18–20°C). Sixteen survived to hatching, which occurred between 28 July and 7 August. Each larva was preserved on the day of hatching. The hatchlings ranged from 12.2 to 13.6 mm SVL (\( \bar{x} = 12.8 \) mm) and 18.9 to 22.4 mm total length (\( \bar{x} = 20.7 \) mm). The female found with the clutch was judged to be the parent. Her flaccid ovaries contained oocytes up to 1.1 mm in diameter, plus many atretic follicles distinguished by their orange pigmentation; each of her convoluted oviducts was 1.2 mm in diameter.

The previous year, on 28 August 1973, 11 hatching larvae were found together in an excavation of loose gravel in the streambed of a different headwater tributary of Alarka Creek. These larvae were similar in size and morphology to those reared in the laboratory; excluding 2 individuals injured in collection, the remaining 9 hatchlings ranged from 12.0 to 12.8 mm SVL (\( \bar{x} = 12.4 \) mm) and from 17.9 to 19.2 mm total length (\( \bar{x} = 18.5 \) mm). If these larvae are considered the progeny of a single clutch, a large female (115 mm SVL) found in the excavation with them, and having spent reproductive organs, was presumably the parent.

Both field clutches had far fewer individuals than predicted from the size-fecundity regression. The discrepancy may have arisen in part from mortality during embryonic development or from my failure to locate all of the members of a clutch. It is also possible that females do not deposit all of the eggs yolked in the ovaries during a given cycle, as suggested by the presence of atretic follicles in the females found with the clutches.
DISCUSSION

In the Cowee Mountains the reproductive cycle of G. porphyriticus is keyed to a summer oviposition period, though individual females apparently do not oviposit on a strictly annual basis. The few egg clutches of this species observed elsewhere by others have been found in October (hatchlings) on Mt. Mitchell, North Carolina (Bishop, 1924), in August (early embryos) in Pennsylvania (Green, 1925), and in July (early embryos) and August (late embryos) on Whitetop Mt., Virginia (Organ, 1961). Bruce (1972) indicated a summer oviposition period in populations of G. porphyriticus in the Blue Ridge and Piedmont, but left the timing of the female cycle unresolved for populations in the Nantahala and Balsam mountains. The suggestion that oviposition usually occurs outside the summer months in the latter populations was probably in error, resulting from my failure to consider nonannual reproductive schedules. Bishop’s (1941) uncertainty about the extent of the egg-laying season of G. porphyriticus in New York may have stemmed from the same circumstance, yet his estimate of a spring and summer oviposition period is probably accurate. Thus, there is no convincing evidence of any significant geographic variation in the egg-laying season of G. porphyriticus; in widely-separated populations oviposition appears to be concentrated in the warmer months, with hatching occurring in late summer or autumn.

The male reproductive cycle shows a similar uniformity among populations of G. porphyriticus. The timing of the spermatogenic cycle in Cowee males is essentially the same as in other populations of the southern Blue Ridge (Bruce, 1972). Moreover, the observation of spermatozoa in the vasa deferentia from early autumn through late spring in males of all these populations was identical to findings on New York males of G. porphyriticus (Dieckmann, 1927; Bishop, 1941). Whether mating is restricted to a narrower period within this interval is unknown.

The larval period of G. porphyriticus is undoubtedly prolonged, but its extent is not known. In view of the absence of size classes in large samples taken in the Cowees, Bishop’s (1941) estimate of a 3-year larval phase, based on size classes identified in small samples, is unconvincing. If hatching is concentrated in late summer and autumn, then the continuity of larval size distributions may be largely an effect of variation in larval growth rates. Metamorphosing individuals of G. porphyriticus have been found only in the summer in the Cowee and other southern Blue Ridge populations. In New York Bishop (1941), in reporting a more extended period (14 March–1 September), suggested that metamorphosis may occur at any time of the year.

Although many of the life-history characters of G. porphyriticus show negligible geographic variation, there are pronounced differences in adult body size among southern Blue Ridge populations that are nowhere more striking than in the Cowee Mountains. The small morph that occupies the southeastern Cowees is similar in body size and pigmentation to the Blue Ridge escarpment and Piedmont representatives of the species; as the southeastern Cowee Mountains are broadly contiguous with the Blue Ridge, the populations of G. porphyriticus of this region are considered a relatively homogeneous assemblage constituting a single species. The large morph of the northwestern Cowees is similar in size and pigmentation to the form found in the Nantahala Mountains to the west, across the Little Tennessee Valley, and these 2 groups of populations appear to be conspecific. Within the Cowee range the boundary between the small and large morphs is at or near Watauga Gap; although no specimens have been taken in searches made at this gap, where suitable habitat is scarce, the small form occurs at Cullowhee Gap 7 km to the southeast and the large form at Brushy Fork 5 km to the north. As there is no evidence that the 2 morphs either intergrade or coexist, it ap-
pears that they may have differentiated to a degree that has led to reproductive isolation but is not sufficient to allow coexistence, such that they replace one another along a sharply-defined boundary. Whether the 2 should be distinguished taxonomically is uncertain, inasmuch as they have not been adequately studied elsewhere where their ranges approach or adjoin; e.g., at low elevations generally in the Little Tennessee Valley, and particularly along the low divide joining the Blue Ridge and southern end of the Nantahala Mountains. Moreover, the relationships among the Blue Ridge—Cowee—Nantahala populations and others nearby in the Balsam, Great Smoky, Cheoah, Unicoi, and Snowbird mountains are unclear. These problems are currently under study.

Whatever the genetic relationship of the 2 Cowee morphs of *G. porphyriticus*, the differences in adult body size, age at maturity, and fecundity also require an ecological interpretation. The optimum age at 1st reproduction of an organism is believed to be dependent on the ratio of juvenile to adult survivorship, growth rates, and the body size-fecundity relationship; if survivorship and individual growth rates are higher for immature than mature individuals, and if fecundity increases with body size, then selection may favor a delay in maturity to take advantage of the larger clutch sizes (even at reduced reproductive effort) and greater opportunities for parental care at larger body sizes (Williams, 1966; Bell, 1976; Stearns, 1976).

Among the salamanders intraspecific variation in age at maturity is particularly well-documented in *Desmognathus ochrophaeus* (Tilley, 1973, 1974, in press) and *Notophthalmus viridescens* (Healy, 1974). These investigators postulated that the observed variation in both species is, at least in part, adaptive, and causally related to environmental gradients over which the species are distributed. The variation in adult body size associated with age at maturity and fecundity among the Cowee populations of *G. porphyriticus* cannot be correlated with an environmental gradient within this small mountain range. Yet as the small morph in the southeast is clearly allied to populations in the nearby Blue Ridge and adjacent Piedmont, and the large morph in the northwest to populations in the Nantahala Mountains, the life-history dichotomy can be examined in this larger context. As the areas now occupied by the size morphs of *G. porphyriticus* are each heterogeneous, and as the 2 morphs overlap considerably in altitudinal distribution, it is unlikely that the life-history differences are direct, non-genetic, physiological responses to present environments. They are instead considered to be adaptive, evolved under conditions of past isolation during episodes of more extreme climates. As suggested earlier (Bruce, 1972), early maturity and small adult body size of the small morph may have been selected for under conditions of repeated cycles of local extinction and recolonization in often marginal habitats along a fluctuating range boundary, wherein populations were often in an expanding phase following drastic reductions in numbers. In contrast, the large morph, occupying more predictable, less severe environments in interior ranges of the southern Blue Ridge, may have maintained more stable populations nearer the limit set by resources, in which the advantages of delayed maturity and large adult size could be more effectively realized. Differences in body size-fecundity regressions between the small and large morphs, which were earlier interpreted as differential female reproductive investments (Bruce, 1972), were not clearly demonstrated in the present study, partly because of inadequate samples of gravid females. Also, as such comparisons represent just one component of reproductive effort, they need to be augmented by other information, particularly the periodicity of reproduction and the costs of yolkling, ovarian retention, and brooding of egg clutches.

It is noteworthy that the larvae of the 2 size morphs of *G. porphyriticus* metamorphose at nearly the same size. Appar-
ently there are selective pressures for retaining a lengthy larval phase and large metamorphic size which are independent of those acting on age of 1st reproduction. This may be a consequence of habitat differences between the pre- and postmetamorphic phases. The cool springs and headwater streams inhabited by larvae are extremely stable; effects of drought are usually slight, and annual temperature variation is often only 2°–3°C. Although metamorphosed *G. porphyriticus* are highly aquatic salamanders that also occupy springbrooks, they are nevertheless more terrestrial than the obligatorily aquatic larvae. These relationships suggest that environmental stresses (warming, drying) may have greater effects on survivorship and growth in the postmetamorphic phase than in larvae, the latters’ existence remaining relatively secure, with selection thereby furthering retention of a long larval period while effecting early reproduction and consequent small body size in postmetamorphic individuals. Such an interpretation of the origin of the small morph is consistent with Murphy’s (1968) hypothesis of life-cycle evolution in organisms having a safe juvenile [= premetamorphic] life and an uncertain adult [= postmetamorphic] existence. However, a more complete picture of the ecology of *G. porphyriticus*, including information on survivorship and individual growth rates in both phases of the life cycle, is needed before the variation in reproductive biology of this species can be adequately evaluated.

Acknowledgments.—I thank my wife and children for accompanying me on many field trips and assisting in the collection of specimens. Wayne Richard prepared the histological sections of testes. I thank D. Bruce Means, Stephen G. Tilley, and an anonymous reviewer for reading the manuscript and providing suggestions for its improvement.

Note added in proof: Statements in the Introduction need to be revised in light of the discovery of a new species of *Gyrinophilus* in West Virginia (Besharse and Holsinger, *Copeia* 1977:624–634).

Literature Cited


Received: 23 November 1976
Accepted: 28 February 1977

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