Ecological Distribution of the Salamanders Gyrinophilus and Pseudotriton in a Southern Appalachian Watershed
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Source: Herpetologica, Vol. 59, No. 3 (Sep., 2003), pp. 301-310
Published by: Herpetologists' League
Stable URL: http://www.jstor.org/stable/3893607
Accessed: 14/05/2011 11:48

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ABSTRACT: The stream-type larval forms of the hemidactyliine plethodontid salamanders Gyrinophilus porphyriticus, Pseudotriton montanus, and P. ruber show subtle interspecific variation in pigmentation and body proportions. I tested the hypothesis that morphological divergence is correlated with adaptive diversification in habitat selection by evaluating the ecological distribution and habitat affinities of larvae of these species in the Chattooga River watershed of the southern Blue Ridge Physiographic Province. Pseudotriton montanus was observed in a single habitat, a bottomland swamp in the floodplain of a third-order stream. Both G. porphyriticus and P. ruber showed an affinity for springs, although the latter had a wider distribution in higher-order streams and small ponds. In springs, larvae of G. porphyriticus showed a greater preference for rheocrenes and a proclivity for burrowing in the coarse substrates of these habitats; in contrast, larvae of P. ruber were more common in limnocrenes and helocrenes, which have finer substrates, and were usually observed among decaying leaves or beneath surface rocks and logs. The habitat associations and behaviors documented herein reinforce earlier interpretations of the adaptive significance of morphometric variation among larvae of the three species.

Key words: Gyrinophilus porphyriticus; Habitats; Larvae; Plethodontidae; Pseudotriton montanus; Pseudotriton ruber; Salamanders

SALAMANDERS of the related genera Gyrinophilus and Pseudotriton have a predilection for springs, seepages, and small headwater streams, and some members of the former genus are adapted to caves. Oviposition occurs in underground sources or subsurface channels of these habitats, such that egg clutches have seldom been observed for any of the species (Petranka, 1998). Larvae, however, are frequently encountered in the outflow channels of springs and seeps and may disperse downstream into higher-order streams as well as to ponds, swamps, and bogs. In a recent morphometric study of larvae of four species of Gyrinophilus, Pseudotriton, and Stereochilus, Birchfield and Bruce (2000) showed that, within the former two genera in the populations evaluated, P. ruber has a robust morphology (greater girth, larger head, thicker limbs) in comparison with the more gracile body plan of P. montanus. Gyrinophilus porphyriticus has the most slender habitus of the three species. There is a trend toward limb attenuation in P. montanus, whereas G. porphyriticus has the shortest limbs. The latter has smaller eyes than either species of Pseudotriton. These authors suggested that variation in morphology reflects adaptive diversification in habitat utilization, with the more generalized P. ruber using the widest range of habitats, in contrast to the preference of P. montanus for lowland and lentic habitats and that of G. porphyriticus for subsurface habitats in upland streams and springs. However, Birchfield and Bruce (2000) provided no quantitative data on variation in larval habitat affinities among these species.

Birchfield and Bruce (2000) collected many of their samples in the Chattooga River watershed, in an area around the common boundary of Georgia, North Carolina, and South Carolina near the southern margin of the southern Blue Ridge Physiographic Province. The present study was designed to evaluate the ecological distribution of larval P. montanus, P. ruber, and G. porphyriticus in lotic and lentic habitats of the Chattooga watershed, in order to test the hypothesis that the documented interspecific variation in
morphology is functionally correlated with the pattern of diversification in habitat affinities among larvae of these species.

Materials and Methods

Study Area

The axis of the Chattooga watershed trends from northeast to southwest for some 60 km, extending from Whiteside Mountain (elevation 1502 m) on the Blue Ridge Divide to the confluence of the Chattooga and Tallulah Rivers at Tugaloo Lake (spillway elevation 272 m), at the boundary of the southern Blue Ridge and Piedmont (Fig. 1). Over much of its course, the river itself lies close to the southeastern boundary of the watershed known as Chattooga Ridge. Thus, most of the major tributaries arise along the northwestern boundary and flow to the southeast to discharge into the main stream.

The climate of the Chattooga is relatively mild and very moist. Precipitation, mainly in the form of rain, decreases downward along the elevational gradient, from 2120 mm annually near the crest of the Blue Ridge at Highlands, NC (1170 m elevation), to 1850 mm in the southwest at Clayton, GA (550 m elevation), to 1630 mm in the southeast at Long Creek, SC (518 m elevation) (NOAA, 1996-1999). Precipitation is distributed relatively uniformly throughout the year. The high precipitation supports rich deciduous and deciduous/coniferous forests that vary in composition according to elevation, slope, and aspect (DuMond, 1970).

Methods

Field work was carried out from 1995-2002. The present study was a component of an inventory by the author of the herpetofauna of the Chattooga watershed, itself part of a multi-investigator scientific study of the Chattooga sponsored by the USDA Forest Service. Sampling was concentrated in sections of the Chattooga within the Chattahoochee (GA), Nantahala (NC), and Sumter (SC) National Forests. In keeping with the goals of the general study, an attempt was made to sample uniformly throughout the watershed, but mainly within the National Forest boundaries, which include most of the watershed. Given the 7-yr term of the study, most areas of the watershed were searched on multiple occasions.

Many localities for *Gyrinophilus* and *Pseudotriton* were recorded in the general herpetofaunal inventory. However, numerous field searches were directed solely at members of these genera and were focused on springs and headwater streams. Such habitats were identified from topographic maps and ground reconnaissance and were selected for investigation based on proximity to roads and trails. All such accessible habitats were searched, regardless of hydrologic features. In addition, a special attempt was made to locate swamp habitats in the bottomlands of the larger streams in order to determine the occurrence of *P. montanus*. Although the search effort was directed at larval salamanders, the numbers of all *Gyrinophilus* and *Pseudotriton* were recorded. Searches for salamanders in springs and streams were made by turning rocks and logs, raking substrate materials, and excavating loose rock and gravel. A dipnet was used to capture salamanders in deeper, quieter waters. Many sites were searched on just one occasion; others were visited on two or more days and on a schedule that minimized recapture (and recounting) of individuals. Although small numbers of larvae were collected and preserved, I released the majority, but I often held them for short periods until the end of a subsequent sampling bout at a given site.

Aquatic habitats supporting larvae of the three species were initially characterized as “pond” and “stream.” Ponds included a number of lentic habitats, including natural woodland pools, sphagnum bogs, swamps, and beaver ponds. Streams were classified by branching order according to the Horton-Strahler system (Morisawa, 1985). In this system, fingertip tributaries are designated first-order, and successive higher-order categories are formed by the confluence of two stream segments of the same order. Because of the habitat associations of *Gyrinophilus* and *Pseudotriton*, I identified an additional lower-order category, order 0, for headwater springs at the origins of first-order streams and for isolated seepages. Stream orders were determined by on-site inspection combined with study of 1:24,000 USGS topographic maps.

The forest type at each site was determined from vegetation maps developed for the
FIG. 1.—Key localities for Gyrinophilus porphyriticus, Pseudotriton montanus, and P. ruber in the Chattooga watershed: (1) Tugaloo Ramp Road, lowermost sites for G. porphyriticus and P. ruber; (2) Whetstone Swamp, the only known site for P. montanus in the Chattooga; (3) Ammons Branch spring cluster; (4) Henson Branch spring cluster; (5) Whiteside Mountain, highest sites for G. porphyriticus and P. ruber.
Chattooga watershed by the USDA Forest Service, in conjunction with on-site evaluation and in reference to the vegetation types of DuMond (1970).

Springs were characterized according to their discharge features and gradient (Lindegaard, 1995) as follows. (1) Rheocrenes discharge over small areas and immediately form first-order streams; they are characteristic of narrow ravines. (2) Limnocrenes discharge into small, pond-like basins of relatively still water, the outflows forming the first-order streams. They tend to form in the floodplains of larger streams, often at the base of a slope along the floodplain boundary. (3) Helocrenes are formed where ground water discharges over relatively large areas, forming wide channels consisting of slow-moving, thin sheets of water, which eventually narrow to form the first-order streams. Helocrenes and their first-order outflow channels tend to occur in broader ravines or in relatively flat areas along the length of second- and higher-order streams.

To evaluate habitat associations of larval *G. porphyriticus* and *P. ruber* in the several categories of spring habitats, presence-absence data were subjected to two-way and three-way G-tests of independence and a chi-square McNemar test for symmetry. Significance was evaluated at $\alpha = 0.05$ in all tests.

Substrate composition was evaluated semi-quantitatively for a number of spring habitats. First, the coverage by larger particles (boulder, cobble, large pebble) was estimated as high, moderate, low, or absent. Then an area was cleared of these large particles and approximately 1 kg (wet weight) of the base substrate was transferred with a trowel to a plastic bag. Two or three such samples were taken within the boundaries of a given site. Upon return to the laboratory, each substrate sample was air dried on newspaper. Following drying, any particles larger than 16 mm (small pebble) were removed by hand and weighed, and the residue was shaken in a series of graduated sieves. Mesh sizes of sieves were 4.00, 2.00, 0.50, and 0.063 mm, which separated medium and coarse gravel (4–16 mm), fine gravel (2–4 mm), very coarse and coarse sand (0.5–2.0 mm), very fine to medium sand (0.063–0.5 mm), and silt and clay (<0.063 mm). Dry sieving does not provide for complete separation of the silt /clay component from larger particles (Cummins, 1962); thus, the results are considered biased against this category. After sieving, the components were weighed to the nearest 0.01 g. Data of the separate trowel samples of each site were pooled in calculating the percentage values.

As the methodology was semi-quantitative, the results cannot provide a statistically valid evaluation of variation in substrate components among habitat categories. Instead, the objective was to identify trends in variation in substrate among habitats utilized by *Pseudotriton* and *Gyrinophilus*. Habitats included in the substrate analysis were all those in which at least 20 larvae of *P. ruber* or 10 larvae of *G. porphyriticus* were observed. I used different criteria for the two species because of the greater abundance of the former throughout the watershed. In addition, the single habitat of *P. montanus* was included.

**RESULTS**

**The Distribution of Gyrinophilus and Pseudotriton in the Chattooga**

Both *G. porphyriticus* and *P. ruber* occur on the northwest slope of Whiteside Mountain, the highest peak in the watershed at 1502 m. *Gyrinophilus porphyriticus* apparently extends higher onto the mountain than *P. ruber*; I observed adults of the former species at several sites at the base of dripping rock faces along the old summit road, now a trail, from 1355 to 1440 m. Other researchers have noted the occurrence of *G. porphyriticus* in these habitats (Bernardo, 1994; Tilley, 1980). In addition, I found larvae at 1340 m in a first-order stream originating below the gap between the main massif of Whiteside and its northeastern spur, known as Devils Courthouse.

In contrast, *P. ruber* has a more restricted distribution on Whiteside. My only records are two larvae, one each on 6 March and 17 April 2000, collected by dipnet from a leaf-choked roadside ditch adjacent to the Whiteside trailhead parking lot at 1340 m elevation. On the later date, the ditch was crowded with egg clutches of *Ambystoma maculatum*. Although I have never observed *P. ruber* in the drainage system supporting *G. porphyriticus* higher on the mountain, given that adults of *P. ruber*...
wander extensively on land, it would not be unusual to find adults at higher elevations during their spring and summer terrestrial phase.

At the opposite end of the watershed, I searched intensively in a small stream and associated seeps on the steep, east side of Tugaloo Lake, along Tugaloo Ramp Road. Although several searches were made, single larvae only of both *P. ruber* and *G. porphyriticus* were observed in these habitats at elevations of about 400 m, within 1 km of the lake.

Between these limits, *P. ruber* and *G. porphyriticus* were found throughout the watershed. Both species occur in a wide range of forest types, broadly characterized as white pine-Canadian hemlock-upland hardwood, cove hardwood, and several variants of mixed oak and oak-hickory (white oak-chestnut oak-hickory, chestnut oak-white oak-northern red oak). I detected no obvious correlation or segregation of these species according to forest type. Watercourses supporting populations of either species are often bordered by dense stands of ericaceous shrubs, including *Rhododendron maximum*, *Kalmia latifolia*, and *Leucothoe axillaris*.

Very few stands of bottomland hardwood forest (designated "bottomland hardwood-yellow pine") are plotted on the Chattooga vegetation maps. The best example of this vegetation type is a bottomland swamp that grades into a Sphagnum bog in the floodplain of Whetstone Creek, where red maple (*Acer rubrum*) is the dominant canopy species. Grasses border the swamp edge, and the adjacent floodplain is covered with a heavy understory of *Leucothoe* and *Smilax*. Sampling here, at an elevation of 480 m, revealed the only known population of *P. montanus* in the watershed. Searches of other swamp and bog habitats in floodplains along the Chattooga and its tributaries that supported different forest communities yielded only *P. ruber*.

**Overlap in the Distribution of Gyrinophilus and Pseudotriton**

The occurrence of larvae of the three species in different habitat categories (Table 1) is biased in that a more intensive sampling effort was directed at springs and first-order streams. The higher incidence of *P. ruber* versus *G. porphyriticus* in second- and third-order streams may be a consequence of higher population densities of *P. ruber* generally. However, the presence of *P. ruber* in pond habitats, where *G. porphyriticus* was never observed, probably reflects the tolerance of *P. ruber* to a greater range of habitats than *G. porphyriticus*.

The usual microhabitats of larval *P. ruber* in higher-order streams were leaf packs in silted pools along the stream margins. The entry of some larvae of *P. ruber* from small tributaries, containing the oviposition and hatching sites, into appropriate habitats in the larger streams may be a natural aspect of the behavioral ecology of this species, as is the colonization of empty springs from these streams. The occurrence of *P. ruber* larvae in some isolated ponds suggests that oviposition occurs in subsurface channels in the banks of these habitats.

Observations of *G. porphyriticus* in larger streams were less frequent. However, intensive sampling of large streams will usually reveal low incidences of this species, as shown in an earlier study on East Fork Overflow Creek, a third-order stream in the upper reaches of the Chattooga watershed (Bruce, 1983). Monthly sampling over a 1-yr period yielded 1287 larval plethodontid salamanders, including 54 *P. ruber* and 3 *G. porphyriticus*.

Inasmuch as springs and their first-order outflow channels dominated the habitat categories of both *P. ruber* and *G. porphyriticus*, I utilized presence/absence data to evaluate: (1) interspecific association of the two species in these habitats, (2) difference between the species in frequency of utilization of such habitats, and (3) difference between the species in utilization of the three categories of spring habitats. In the analysis were all

**Table 1.—Occurrences of larval Gyrinophilus and Pseudotriton in the Chattooga watershed according to habitat category. Stream habitats are subdivided according to a modification of the Horton-Strahler system, as described in the text.**

<table>
<thead>
<tr>
<th>Species</th>
<th>Pond</th>
<th>0/1</th>
<th>1</th>
<th>2</th>
<th>3</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pseudotriton montanus</em></td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td><em>Pseudotriton ruber</em></td>
<td>9</td>
<td>51</td>
<td>3</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td><em>Gyrinophilus porphyriticus</em></td>
<td>0</td>
<td>35</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>
habitats that included either the headwater spring only or (usually) the spring and a short section of the first-order stream immediately below the springhead. I included data from all sites where larvae of both species were observed, regardless of sample size or sampling intensity. However, for habitats lacking one or both species, the habitat was retained only if multiple intensive searches convinced me that the missing species was (or were) absent or at least extremely uncommon. The few habitats lacking both species were springs having low discharge rates and/or very short channels issuing into higher-order streams. I assume that the habitat representation in the analysis is adequately randomized in that I searched all spring habitats that I could readily access, without regard to hydrology, substrate, vegetation, or other features. The frequencies of species occurrence are given in Table 2.

The initial tests were based on presence/absence data of all 0-order habitats, without regard to hydrologic category, and were designed to test independence in habitat association between larvae of *P. ruber* and *G. porphyriticus* in springs (Table 2, pooled data). Although the diagonal product (22 × 6 = 132) is well below that of the off-diagonal (13 × 29 = 377), the difference is marginally non-significant (G = 3.605, df = 1, P = 0.058), suggesting that larvae of the two species may be distributed independently of one another. A McNemar symmetry test on the number of habitats occupied by only one or the other species, that is 29 (*P. ruber*) versus 13 (*G. porphyriticus*), yielded a significant difference (χ² = 6.09, df = 1, P = 0.014), indicating that larvae of *P. ruber* are more widely distributed than those of *G. porphyricus* across the range of spring habitats in the Chattooga watershed.

Such a difference may reflect predilections of either species for particular categories of springs, as well as the frequencies of the latter within the set of springs that was sampled. To test the affinity hypothesis, I subdivided the data according to type of spring, i.e., helocrene, rheocrene, limnocrene (Table 2) and conducted a three-way test of independence of habitat type and the presence/absence variables of the two species. The result was highly significant (G = 43.92, df = 7, P < 0.001), indicating differences in affinities for the three types of springs in one or both species. Two-way tests showed that the habitat effect applied to both species (*G. porphyriticus*: G = 19.17, df = 2, P < 0.001; *P. ruber*: G = 25.39, df = 2, P < 0.001). It is concluded that larvae of *P. ruber* have a greater preference for helocrenes and limnocrenes and those of *G. porphyriticus* for rheocrenes.

Variation in distance between springs might violate the assumption of independence of replicates in the above frequency tests. However, my experience suggests that distances between empty and occupied springs are short in this watershed and that empty springs are readily accessible for colonization through either upstream migration of larvae and postmetamorphs or overland movements of the latter, such that the presence or absence of either species is determined largely by habitat quality. I examined the latter hypothesis indirectly in the two largest clusters of springs sampled: (1) seven small tributaries of Ammons Branch (a second-order stream) spaced over a distance of only 0.3 km along the southwest side of this stream and (2) seven short tributaries located on either side of a 0.25 km stretch of Henson Branch (also a second-order stream). The close spacing should minimize a distance effect. The data support the habitat quality hypothesis relative to the distribution of larvae in limnocrenes, helocrenes, and rheocrenes (Table 3). Thus, at Ammons Branch larvae of *P. ruber* only were observed in the single limnocrene. The two most extreme rheocrenes, issuing into high-gradient channels with coarse substrates, yielded only *G. porphyriticus*. In the two other rheocrenes and the two helocrenes, both species were encountered. Intensive searching
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TABLE 3.—Numbers of larvae of Gyrinophilus porphyriticus and Pseudotriton ruber observed in the Ammons Branch and Henson Branch spring clusters, with numbers of metamorphosed individuals shown in parentheses. Springs are numbered upstream to downstream relative to the main streams.

<table>
<thead>
<tr>
<th>Site</th>
<th>Category</th>
<th>G. porphyriticus</th>
<th>P. ruber</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ammons Branch</td>
<td>2nd-order stream</td>
<td>0 (2)</td>
<td>2 (1)</td>
</tr>
<tr>
<td>Spring 1</td>
<td>Helocrene</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td>Rheocrene</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>3</td>
<td>Limnocrene</td>
<td>0</td>
<td>14</td>
</tr>
<tr>
<td>4</td>
<td>Rheocrene</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>5</td>
<td>Rheocrene</td>
<td>2 (3)</td>
<td>0</td>
</tr>
<tr>
<td>6</td>
<td>Rheocrene</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>7</td>
<td>Helocrene</td>
<td>1 (1)</td>
<td>1</td>
</tr>
<tr>
<td>Henson Branch</td>
<td>2nd-order stream</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>Spring 1</td>
<td>Limnocrene</td>
<td>0</td>
<td>4</td>
</tr>
<tr>
<td>2</td>
<td>Limnocrene</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>3</td>
<td>Rheocrene</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>4</td>
<td>Helocrene</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>5</td>
<td>Helocrene</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>6</td>
<td>Helocrene</td>
<td>0</td>
<td>12</td>
</tr>
<tr>
<td>7</td>
<td>Helocrene</td>
<td>2</td>
<td>1</td>
</tr>
</tbody>
</table>

in Ammons Branch itself yielded only two larvae and one adult P. ruber, plus two adults of G. porphyriticus. Similar results were obtained at Henson Branch. Larvae of P. ruber only were observed in both limnocrenes and three of the helocrenes. A fourth helocrene had a coarser substrate and supported both species. The single rheocrene also yielded both species. Larvae of P. ruber only were dipnetted in leaf packs along the edges of Henson Branch.

Substrate Characteristics

As shown in Table 4, the substrates of the four larval habitats occupied exclusively by P. ruber (sites 2–5) were characterized generally by the absence or paucity of large particles (gravel and larger) and a preponderance of sand, interspersed with smaller quantities of silt/clay. In all of these habitats, larvae of P. ruber were usually found on the surface of the mineral substrate hidden among decaying leaves and other plant debris. Of special interest, site 2 consisted of a small, silted pond bordered by a sandy-bottomed seepage. Larvae of P. ruber were observed throughout. Part of the discharge of the seep was intercepted by the pond, while the rest flowed through a floodplain of West Fork Overflow Creek. This is reflected in the differential proportions of sand and silt/clay in the two substrate samples from this site. The substrate of the pond basin was heavily silted, whereas that of the shallow border with the seep was primarily sand.

In contrast, habitats of larval G. porphyriticus tended to have higher proportions of larger particles (coarse sand, gravel, pebble) and moderate to high incidences of larger rocks. This type of substrate is conducive to burrowing; the majority of larvae of G. porphyriticus were detected by lifting large rocks and logs and excavating saturated beds of gravel, pebble, and larger particles to depths of several centimeters. Of the four habitats of G. porphyriticus listed in Table 4, three also

TABLE 4.—Substrate characteristics of selected habitats of larval Pseudotriton and Gyrinophilus. Sites 2 and 9 are subdivided, as explained in the text.

<table>
<thead>
<tr>
<th>Site no., category</th>
<th>No. of larvae</th>
<th>Substratum category¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>1, pond</td>
<td>40 2 0</td>
<td>B/C/P 1 2 3 4 5 6</td>
</tr>
<tr>
<td>2, pond</td>
<td>0 19 0</td>
<td>A 0 0 0 0 0 0.146 0.854</td>
</tr>
<tr>
<td>3, helocrene</td>
<td>0 6 0</td>
<td>A 0 0 0.001 0.012 0.262 0.707 0.018</td>
</tr>
<tr>
<td>4, helocrene</td>
<td>0 20 0</td>
<td>A 0 0.001 0.012 0.262 0.707 0.018</td>
</tr>
<tr>
<td>5, helocrene</td>
<td>0 21 0</td>
<td>L 0 0.016 0.036 0.292 0.637 0.018</td>
</tr>
<tr>
<td>6, helocrene</td>
<td>0 22 5</td>
<td>L 0.046 0.061 0.093 0.325 0.460 0.015</td>
</tr>
<tr>
<td>7, helocrene</td>
<td>0 16 0</td>
<td>M 0.278 0.121 0.112 0.232 0.254 0.004</td>
</tr>
<tr>
<td>8, helocrene</td>
<td>0 11 0</td>
<td>M 0.098 0.107 0.061 0.269 0.463 0.003</td>
</tr>
<tr>
<td>9, rheocrene</td>
<td>0 10 0</td>
<td>H 0.253 0.249 0.052 0.135 0.308 0.005</td>
</tr>
<tr>
<td>10, rheocrene</td>
<td>0 12 0</td>
<td>L 0.215 0.215 0.118 0.206 0.233 0.012</td>
</tr>
</tbody>
</table>

¹ B/C/P (boulder/cobble/large pebble): A = absent, L = low, M = moderate, H = high. Numbers: Proportions of mass of 1 = small pebble, 2 = medium-coarse gravel, 3 = fine gravel, 4 = very coarse-coarse sand, 5 = medium-very fine sand, 6 = silt-clay.
supported populations of *P. ruber*; larvae of
the latter were found under rocks, logs, and in
leaf packs, but invariably on or near the
surface, and were not encountered during
evacuations of the stream bed. Habitat 9 was
also of special interest. It consisted of an
isolated seepage, issuing as a rheocrene and
running on the surface about 25 m before
disappearing underground for most of its
remaining distance (approximately 100 m)
before discharging into a second-order stream.
Whereas the upper half of the seepage was
heavily bedded with loose rock and flowed
over a moderate gradient, the lower half was
a sluggish, silted, low-gradient channel that
was strewn with decaying leaves. Of the larvae
observed here, all 10 *G. porphyriticus* were
located in the upper section, while the 12 *P.
ruber* were found in the lower reach, with no
overlap between the species.

The single habitat where *P. montanus* was
observed consisted of a bottomland swamp
and adjacent *Sphagnum* bog. Substrate sam-
pies were taken only from the former; the
material was primarily silt/clay with a small
admixture of mainly fine sand. Larvae of *P.
montanus* were taken by pulling a dipnet
through decaying plant debris on the bottom
of the swamp and bog.

**DISCUSSION**

In terms of larval ecology, *P. ruber* is the
most widely-distributed of the three species of
*Pseudotriton* and *Gyrinophilus* in the Chat-
tooga watershed, occurring in a variety of lotic
and lentic habitats. *Pseudotriton montanus* is
at a limit of its range in the Chattooga and is
restricted to bottomland swamp-forest habitat
that represents its major adaptive zone in the
southeastern United States (Means, 2000).
The only documented locality for *P. montanus*
in the Chattooga was identified initially from
the vegetation maps as one of very few stands
of bottomland hardwood forest in the water-
shed. Small numbers of *P. ruber* were also
observed here. At nearby Piedmont sites, I
earlier reported nearly complete habitat seg-
ration of *P. montanus* and *P. ruber*, with the
former in lowland and the latter in upland
habitats (Bruce, 1974). However, elsewhere in
the Piedmont, the two species may overlap
considerably (Bruce, 1968). In the southeast-
ern Coastal Plain, Means (2000) found that *P.
montanus* has an affinity for swampy flatwoods
streams and *P. ruber* for streams in ravines,
with no recorded overlap.

Larvae of *P. ruber* occur in small ponds and
higher-order streams, but their principal
habitats are springs and first-order streams,
which also represent the preferred habitats of
larval *G. porphyriticus*. Although the two
species often co-occur in such habitats, they
tend to segregate according to spring category,
with *P. ruber* most frequent in limnocrenes
and helocrenes and *G. porphyriticus* showing
a greater frequency in rheocrenes. Where they
coeexist, larvae of *P. ruber* tend to occur on
finer substrates among decaying leaves or
under surface rocks and logs, whereas those
of *G. porphyriticus* more often occupy sub-
surface channels of percolating water in zones
of coarser substrates.

Many of the springs sampled in this study
were small, and, thus, they may be subject to
episodes of extinction and recolonization by *G.
porphyriticus* and *P. ruber*. Only a few springs
were searched that lacked both species; in each
case, these were springs with low discharge
rates that flowed short distances before either
discharging into a higher-order stream or
disappearing underground. The absence of
larvae in these springs may be, in part, an effect
of drying in drought years. Empty springs
may be recolonized by upstream movements
of larvae and metamorphosed individuals.
Adults of both species move overland as well;
in the Chattooga region, *P. ruber* is more
frequently encountered in terrestrial habitats
than *G. porphyriticus*, which may reflect the
higher population densities of the former
species (Bruce, 1968, 1972, 1978).

Morphologically, Birchfield and Bruce
(2000) suggested that *P. ruber* has the most
generalized larval habitus among members
of the *Gyrinophilus-Pseudotriton*-Stereochnus
clade, which reflects utilization of a broader
habitat range than other species in these
genera. *Pseudotriton montanus* was found to
have a more slender habitus and somewhat
more attenuated limbs than *P. ruber*, which I
interpret as an adaptation that enhances
support and locomotion on the soft, silted
substrates of its favored habitats.

Brandon (1966), in comparing head and eye
proportions of *G. palleucus*, *G. porphyriticus*,
and *P. ruber*, considered the smaller eyes and broader, flatter snouts in *Gyrinophilus* as adaptations for subterranean life. The morphometric analysis of Birchfield and Bruce (2000) showed that the larval morph of *G. porphyriticus* has a more slender body, shorter limbs, and smaller eyes than *P. ruber*; these differences, as well as the paler pigmentation of the former, are suggestive of a subsurface mode of life in the interstitial zone of the stream bed. This interpretation is reinforced by the Chattooga habitat data; larvae of *G. porphyriticus* show a proclivity for zones of helocrenes and rheocrenes (and the first-order streams they give rise to) having coarse substrates. It is often necessary to excavate the substrate to depths of several centimeters to locate larvae.

Although Valentine and Dennis (1964) categorized larvae of *Pseudotriton* and *Gyrinophilus* as “stream type,” they are not actually rheoculous, in that larvae of none of the species ordinarily inhabit riffle areas of fast current. Given that these genera, together with *Stereochilus*, retain the least derived developmental and life history patterns of plethodontid salamanders (Collazo, 1996; Collazo and Marks, 1994; Ryan and Bruce, 2000) and form a relatively basal clade within the family (Larson et al., 2003), the larval adaptive zones of the constituent species should inform the question of the origin of lunglessness in this family. Originally, Wilder and Dunn (1920), later supported by Beachy and Bruce (1992) and Bruce et al. (1994), advanced the hypothesis that lunglessness is a larval adaptation to mountain streams, which serves to decrease buoyancy and facilitate purchase and movement on the stream bottom. Alternatively, Ruben and Boucot (1989) and Ruben et al. (1993) proposed that lunglessness evolved in semi-aquatic or terrestrial plethodontid ancestors, under unspecified ecological conditions that promoted selection for head narrowing, and led to reduced pulmonary efficiency and concomitant selection for the substitution of bucco-cutaneous for pulmonary respiration. Means (2000) identified a possible ecological determinant for such selection as “locomotion in the viscous medium of muck and wet peat” of seepage habitats, as he observed in several Coastal Plain species of plethodontids, including both species of *Pseudotriton* and *Stereochilus marginatus*. It was his contention that the respiratory and hydrostatic functions of lungs in aquatic salamanders inhabiting the open waters of ponds would be maladaptive in shallow, mucky, seepage habitats occupied by many species of aquatic plethodontids. It is, of course, possible that the evolution of lunglessness in plethodontids was an outcome of selection acting along the entire upstream-downstream gradient of lotic ecosystems.

**Acknowledgments.**—I thank G. Birchfield, E. Bruce, S. Freeman, B. Stuart, C. Spencer, and N. Taylor for assistance in the field; D. Tarbox at the Strom Thurmond Institute of Clemson University for producing the map; and C. Beachy for providing valuable comments on the manuscript. The early phase of the study was supported by Challenge Cost-Share Agreement No. 95-03-12 between the USDA Forest Service and the Highlands Biological Station. Additional support was provided by the Highlands Biological Station.

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Accepted: 27 December 2002

Associate Editor: Carl Anthony