An Ecological Life Table for the Salamander *Eurycea wilderae*

**Richard C. Bruce**

Fall and winter samples of *Eurycea wilderae* from a small stream in the Blue Ridge Mountains of southwestern North Carolina provided data for an ecological life table. In this population, oviposition occurred in late winter and early spring, followed by hatching in late spring and early summer. The salamanders then spent 1 or 2 yr as larvae, followed by at least a year as juveniles. Age at first reproduction in both sexes was estimated to be either 3 or 4 yr, but usually the latter, since most individuals metamorphosed at 2 yr. Two morphs of mature males were observed. Males having cirri were smaller than males lacking cirri, suggesting that the variation was ontogenetic.

Age structure was determined from the representation of life-history stages in the samples, after adjustment for early metamorphosis. From the age class estimates, annual survivorship values for the first 3 yr of life were calculated from the ratios of frequencies of successive age classes. For later years I assumed constant postmetamorphic survivorship and estimated this value from the ratio 3 yr to 4 yr and older individuals. Fecundity was determined by dissecting gravid females and calculating a least-squares regression of egg number against snout-vent length. The survivorship and fecundity data allowed completion of the life table and calculation of $R_0$, which was 0.821. Such a low value probably reflects sampling and interpretive errors; otherwise a value of $R_0 < 1.0$ is indicative of a declining population. By making no assumptions concerning $R_0$, but assuming a stable age distribution, mean generation time was calculated as 4.4 yr. Pronounced variation in this and other life-history traits among *E. wilderae* and other Appalachian plethodontids stands in contrast to relative invariance in age at first reproduction in these salamanders.

The principal evolutionary trend in plethodontid salamanders has been a shift from an aquatic mode of life in temperate mountain streams to a more terrestrial existence in both temperate and tropical forests (Dunn, 1926; Wake, 1966). Hairston (1986) has argued that predation is a significant factor in promoting terrestrial adaptations in plethodontids. Sup-

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posedly, the aquatic environment has been more hazardous than the surrounding forest for these salamanders. Organ’s (1961) set of survivorship curves for several species in the genus Desmognathus represents evidence that increasing adaptation to terrestrial life is accompanied by improvements in survivorship in plethodontids. There have been few attempts to determine life tables for amphibians with biphasic life cycles (Wilbur, 1980), mainly because of the difficulty in obtaining unbiased estimates of survivorship across the metamorphic boundary. Life tables for plethodontid salamanders have been determined for several species of Desmognathus (Organ, 1961; Spight, 1967; Tilley, 1980), and for the terrestrial Plethodon jordani (Hairston, 1983). Data of this kind are required for evaluating demographic trends in the adaptive radiation of plethodontids.

The genus Eurycea, of the tribe Hemidactylidae, represents a different plethodontid lineage than either Desmognathus or Plethodon. All of the species of Eurycea have free-living larvae. The southern Appalachian member of the Eurycea bislineata complex has recently been recognized as a full species, E. wilderae Dunn (Jacobs, 1987). Following completion of several studies of this species (then referred to as E. bislineata) in the southern Blue Ridge Mountains (Bruce, 1982a, 1982b, 1985), I decided that E. wilderae was amenable to a demographic study following Michod and Anderson’s (1980) guidelines and using Hairston’s (1983) method for analyzing size distributions. The current study was undertaken to generate an ecological life table for E. wilderae using these procedures, and to interpret the results in the context of the life table data available for other southern Appalachian plethodontids.

**Materials and Methods**

The major part of the study was conducted in Station Creek, a small stream which flows through the grounds of the Highlands Biological Station on the Highlands Plateau in the southern Blue Ridge Mountains, Macon County, North Carolina. An earlier study of E. wilderae at this site (Bruce, 1985) indicated stability of larval population structure over a 3 yr period (1981–83), suggesting that the population was suitable for a demographic study based on age-class analyses. Station Creek lies at an elevation of about 1100 m within a mature hemlock-hardwood forest. A 250 m section of the stream was the main sampling area. This part of the stream is about 1–2 m in width, with midstream depths ranging from a few centimeters to about 0.5 m in some downstream pools.

Most samples were taken from Jan. through early March. Winter sampling was designed to take advantage of the presence of all life history stages in the stream at one time. In E. wilderae in the southern Blue Ridge, metamorphosed individuals generally leave the streams in the spring, returning in autumn after spending the summer on land. By confining the sampling to winter, all life-history stages could be taken in the same habitat, which would not be possible in the warmer months.

Sampling was done using a D-frame dip net. Because larvae and postmetamorphic individuals occupy the same habitats in winter, living under rocks, among gravel, and in leaf packs, I expected that the dip net method would be effective in taking unbiased samples. In collecting, the rim of the net was set firmly against the streambed, and the bottom materials upstream of the opening were vigorously stirred by foot, causing the displaced salamanders to drift into the net. It was necessary to assume that the method was equally effective in collecting all life-history stages.

Using the above method, two major samples were taken in each of two successive winters, 1984 and 1985, yielding four large samples. The salamanders were returned to the laboratory, lightly anesthetized in Chloralose, measured for snout–vent length (SVL) to the nearest 0.1 mm, and assigned to life-history stages on the basis of external criteria. I noted the occurrence of cirri in males and the presence of large yolky oocytes visible through the body wall in gravid females. In the first sample of each year, the salamanders were marked by clipping one toe on each of two feet. They were given a common mark rather than marked for individual recognition. The recapture data were inadequate for reliably estimating population density, as originally intended, and these results are not presented. However, the use of the method is noted because the data have been utilized for other purposes. Following examination in the laboratory, the salamanders were revived in stream water and released near the point of capture.

Each major sample was collected over several days. Because the salamanders were released after each day’s collection, I conducted the collecting-releasing in an upstream direction dur-
ing any one sampling period. It was assumed that upstream movements in winter over the short period of time involved would be slight, and therefore that the chance of collecting an individual twice in any one sample would be minimal. This assumption was upheld by my failure to recapture any marked salamanders within the first sampling interval of each year.

In 1984, samples were collected 25 Jan.–4 Feb. (N = 218) and 22 Feb.–7 March (N = 224). In 1985, sampling was delayed by the nearly complete freezing over of Station Creek. The first sample was taken 2–14 Feb. (N = 204) and the second, 4–7 March (N = 228).

In March 1984 I collected a sample of 50 metamorphosed E. wilderae for dissection from several streams immediately adjacent to Station Creek. This was done to verify reproductive status, to obtain oocyte counts in gravid females, and to examine spent females for residual ova.

In addition, I collected four samples of metamorphosed individuals from Station Creek in the autumn and winter of 1985–86. These were taken because sex and reproductive status were not unequivocally determined for individuals in the 1984 and 1985 winter samples. I later found that the reproductive features of E. wilderae could readily be determined by passing an intense beam of light from a fiber-optics illuminator through the body of an anesthetized individual. This clearly revealed the testes in both immature and mature males, and showed the vasa deferentia (black, coiled) in the latter. Since dissection had shown that mature females were invariably gravid in the autumn, and since gravid females could easily be recognized by external examination, individuals not identified as males by the illumination method were scored as immature females. Dissection of selected specimens confirmed the accuracy of the procedure, which was applied to the 1985–86 samples.

In taking the 1985–86 autumn–winter samples, I decided to collect successive samples of N = 50 or a multiple thereof, for a total of 300 captures. The results were samples of 50 each on 1–25 Oct. and 13–16 Nov. 1985, a sample of 150 on 8–22 Jan. 1986, and a sample of 50 on 21–24 Feb. 1986. The collections were made in Station Creek and from several associated seepages. I used a longer stretch of Station Creek for these collections than in 1984 and 1985. Since a given sample was taken over several days, I designed the collecting and releasing to minimize the chance of recapturing individuals in each sample. However, the succession of four samples undoubtedly included individuals previously captured. Although the sampling was mainly non-destructive, I dissected a number of females to obtain estimates of clutch size as well as a few other individuals to verify reproductive status. Since the area sampled was extensive, such removals should have had little impact on population structure.

Results

Composition of the population in winter.—The makeup of the four winter samples of 1984 and 1985 is shown in Figure 1. Individuals of E. wilderae were scored as larvae, juveniles, or adults. Juveniles were recognized as metamorphosed individuals smaller than the smallest individual which could be identified as a mature male (cirri present) or mature female (gravid). The boundary between juveniles and adults varied somewhat among the four samples, but was necessarily determined separately for each. The adult category included some individuals which could not be readily sexed by external features, but were classed as adults strictly on the criterion of size. Such designations were later shown to be largely accurate on the basis of the more discriminating examination of specimens in the 1985–86 samples.

The size distributions of larvae were either bimodal or skewed, indicating the presence of two age classes, as expected (Bruce, 1985). The frequencies of the two components were estimated by plotting cumulative frequencies of SVL on probability graph paper. The inflexion points of the resultant sigmoid curves represented the breaks between 1 and 2 yr larvae. The proportions of younger: older larvae in these four samples were consistent, ranging from 72:28–77:25%.

The members of the winter samples could then be assigned to the four life-history stages: 1 yr larvae, 2 yr larvae, juveniles, and adults (Table 1). Although the four stages were not strictly age classes, as described below, the correspondence was considered close enough to use the data to test the hypothesis that age structure was stable in the population. A G-test, adjusted with Williams' correction, indicated no significant difference among the four samples in the frequencies of the four stages (G = 5.20, 9 df, P > 0.05). Although the frequencies of juveniles and adults were less in both 1985 sam-
The 1985–86 data on metamorphosed individuals (Fig. 2) provided for a better evaluation of population structure since each individual was unequivocally assigned to a reproductive category. The data revealed the presence of two morphs of mature males, those having cirri and those lacking them. Except for two spent females taken with egg clutches in the Feb. sample, mature females were always gravid, indicating that females oviposit annually. These findings suggested that the unsexed adults in the 1984 and 1985 samples were males lacking cirri.

The Oct. 1985 sample was obviously biased against juveniles and cirrigerous males, suggesting that in the fall migration from forest to stream the non-cirrigerous males and mature females arrive first, followed by juveniles and cirrigerous males. For this reason, I omitted the Oct. sample from the demographic analyses which follow. If the same criteria are applied to the last three 1985–86 samples as to those of the winters of 1984 and 1985, the proportions

Fig. 1. Size-frequency distributions of Eurycea wilderae in the four major samples from Station Creek in the winters of 1984 and 1985. Open squares (<27 mm) = larvae, dark squares = juveniles, squares with pluses = mature cirrigerous males, squares with dark circles = gravid females, open squares (>32 mm) = unsexed adults.
of juveniles and adults (44, 56\% in 1984–85; 47, 53\% in 1985–86) are similar. This further reinforces the conclusion of a stable population structure. However, the actual proportions showed a greater difference between years, mainly because the body size overlap between juveniles and adults could be resolved in the 1985–86 samples. This yielded higher proportions of juveniles than earlier, because juveniles equal to or larger than the smallest adult were correctly scored in 1985–86. In addition, any sex differences in body size contributing to the overlap could be accounted for in the 1985–86 samples. Thus the last three samples of 1985–86 contained 136 (54.4\%) juveniles and 114 (45.6\%) adults.

These juvenile : adult proportions varied according to sex (Table 2). Sex ratios were eval-

**Table 1. Composition of Winter Samples of Eurycea wilderae from Station Creek.** Based on data of Figure 1. Numbers of larvae in each age class were estimated by probability plots of cumulative frequencies. Numbers in parentheses represent percentages of row totals.

<table>
<thead>
<tr>
<th>Collection dates</th>
<th>1 yr larvae</th>
<th>2 yr larvae</th>
<th>Juveniles</th>
<th>Adults</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1984</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>25 Jan.–4 Feb.</td>
<td>124 (56.8)</td>
<td>48 (22.0)</td>
<td>23 (10.6)</td>
<td>23 (10.6)</td>
<td>218</td>
</tr>
<tr>
<td>22 Feb.–7 March</td>
<td>141 (62.9)</td>
<td>42 (18.8)</td>
<td>17 (7.6)</td>
<td>24 (10.7)</td>
<td>224</td>
</tr>
<tr>
<td>1985</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2–14 Feb.</td>
<td>127 (62.2)</td>
<td>42 (20.6)</td>
<td>14 (6.9)</td>
<td>21 (10.3)</td>
<td>204</td>
</tr>
<tr>
<td>4–7 March</td>
<td>147 (64.5)</td>
<td>47 (20.6)</td>
<td>15 (6.6)</td>
<td>19 (8.3)</td>
<td>228</td>
</tr>
<tr>
<td>Total</td>
<td>539 (61.7)</td>
<td>179 (20.5)</td>
<td>69 (7.9)</td>
<td>87 (9.9)</td>
<td>874</td>
</tr>
</tbody>
</table>
eated for all four 1985–86 samples. There was no departure from a 1:1 sex ratio among juveniles, but males tended to predominate among adults. There was a pronounced departure from 1:1 in the Oct. sample, even though only one of the two male morphs was represented. Of the remaining samples, neither of the two smaller (N = 50) ones showed a departure from a 1:1 adult sex ratio, but the large Jan. sample (N = 150) showed a highly significant predominance of males. In the demographic analysis to follow, I have assumed that the difference was real, and have estimated female survivorship from the juvenile : adult proportions of females in the last three samples of 1985–86.

Two types of mature males occur in the Station Creek population: males having cirri projecting from the snout, and those lacking cirri and having enlarged temporal muscles. The cirrurous males tended to be more brightly pigmented (orange) in contrast to the duller (yellow-green) non-cirrurous males. In the fall-winter samples of 1985–86, the Oct. sample had only non-cirrurous males, whereas both morphs were taken in the three later samples (Fig. 2). In these, the mean SVL of non-cirrurous males was greater than that of cirrurous males, and the difference was significant in two of the samples (Table 3).

Age structure of the population.—Individuals have been aged from the estimated date on which they entered the population as eggs. The later winter samples overlapped the beginning of the egg-laying season. Two egg clutches, both attended by the presumed female parent, were observed on 21 Feb. 1986; otherwise, egg clutches have been observed in Station Creek, over a period of several years, from mid-March through the spring months, with hatching larvae first appearing in June and July (Bruce, 1985). For the purpose of assigning ages, it appeared reasonable to consider that the winter sampling period coincided with the pulse of egg-laying. This allowed ages to be assigned to the winter age classes in annual increments from age 0, which simplified the calculation of survivorship.

The frequencies of life-history stages do not represent age-class frequencies because larvae may metamorphose at either 1 or 2 yr after hatching. The best available estimate of the probability of early metamorphosis is 0.0741, with all surviving larvae metamorphosing a year

Table 3. Body Sizes of the Two Morphs of Male Eurycea wilderae at Station Creek.

<table>
<thead>
<tr>
<th>Sample date</th>
<th>Cirri present</th>
<th>Cirri absent</th>
<th>F test*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>x</td>
<td>SD</td>
</tr>
<tr>
<td>13–16 Nov. 1985</td>
<td>6</td>
<td>37.8</td>
<td>2.14</td>
</tr>
<tr>
<td>8–22 Jan. 1986</td>
<td>13</td>
<td>38.7</td>
<td>2.87</td>
</tr>
<tr>
<td>21–24 Feb. 1986</td>
<td>11</td>
<td>36.4</td>
<td>1.91</td>
</tr>
</tbody>
</table>

* n.s., nonsignificant.
** P < 0.01.
*** P < 0.001.
later (Bruce, 1985). Thus the juvenile class in the winter included a few 2 yr as well as 3 yr individuals.

Was the fall and winter juvenile class derived entirely from the metamorphic class of the preceding summer? If it was, the entire juvenile class present in the winter must have been scheduled to mature by next autumn. This would mean that the juvenile class was composed of 2 and 3 yr individuals only. The evidence bearing on the question was inadequate. The size range of metamorphs in this population in late spring and summer was found to be 18–24 mm (Bruce, 1985), whereas juveniles in the fall and winter ranged from 24–36 mm. In the winter of 1984 and 1985 the magnitude of the SVL range of juveniles was similar to that of larger 1 yr plus all 2 yr larvae. However, in 1985–86, where more precise criteria were used, the juvenile size range was greater, particularly among females. The pattern of metamorphosis in this population (Bruce, 1985), where the larger 2 yr larvae metamorphose early (beginning late May), followed by smaller 2 yr larvae and finally (early Aug.) the larger 1 yr olds, would tend to stretch out the juvenile size range by giving the larger metamorphs a head start in postmetamorphic growth. Yet I am skeptical that the smallest female juveniles (25 mm SVL) present in the winter would be able to grow to adult size and produce eggs by the next year. However, since the results provided no real evidence that E. wilderae at Station Creek spend more than 1 yr as juveniles, and accommodate the view of a 1 yr juvenile phase, I have accepted the latter alternative in conducting the demographic analyses.

I considered the data of Table 1 representative of four independent, random samples, in which recaptures of marked salamanders could be disregarded, and pooled the data to obtain the proportions of the four stages, which are given in the last row of the table and carried over to Table 4. It is these values that are used in deriving the remaining frequencies given in Table 4, as follows:

If the probability of metamorphosis in the summer at 1 yr after hatching (i.e., at age 1.5 yr) is assumed to be 0.0741, then by the next winter the proportion of 2 yr larvae among all 2 yr individuals would be 1.0–0.0741 or 0.9259, and the proportion of 2 yr individuals in the population would be 0.2048/0.9259 = 0.2212. To obtain this proportion, 0.0164 needs to be subtracted from the total juvenile frequency of 0.0790 and combined with 0.248, representing the proportion of 2 yr larvae. This leaves 0.0626 as the proportion of 3 yr juveniles. These calculations assume equal survivorship of larvae and juveniles of the same age from summer to winter.

Similarly, under the assumption that E. wilderae spend only 1 yr in the juvenile state, the 3 yr class is a mix of many juveniles and a few adults. The only basis for estimating the proportions is to use the value 0.0741, as defined above, to calculate the ratio of 3 yr juveniles to all 3 yr individuals as 0.9259, yielding a proportion for 3 yr individuals of 0.0626/0.9259 = 0.0676. This requires transferring 0.0050 from the adult frequency of 0.0995 to the 3 yr class, leaving a frequency of 0.0945 for 4 yr and older individuals, which are all considered adults. These transformations, summarized in Table 4, represent my best estimate of age structure for this population.
Survivorship.—Because the winter sampling periods closely coincided with the pulse of egg-laying, calculations of survivorship could be made from age 0 for successive 12 mo intervals. For the first year of life, 0–12 mo, I estimated survivorship from the total number of 1 yr larvae in the 1984 and 1985 winter samples, divided by the product of the total number of mature females multiplied by the average number of eggs in gravid females (see Fecundity below). This calculation gave a survivorship estimate of \( \frac{539}{28 \times 40.9} = 0.4707 \). It covers the period of oviposition, incubation (wherein the eggs are attended by the female parent), hatching, dispersal of hatchlings from the nest, and the first few months of free-living larval existence.

Using the values of Table 4, survivorship from 12–24 mo was calculated as \( \frac{0.2212}{0.6167} = 0.3587 \). Similarly, survivorship from 24–36 mo was \( \frac{0.0676}{0.2212} = 0.3056 \). Both of these intervals, though mainly the latter, included survivorship through the metamorphic period. The lower survivorship in the second and third years vs the first may represent a sampling error, but also probably reflects variation associated with the different life-history events covered by these periods.

For ages beyond 36 mo, I estimated survivorship separately for each sex from the 1985–86 samples. The totals for juveniles and adults in the last three samples (Table 2) provided the frequency estimates, which were carried to the total row of Table 5. To partition these frequencies by age, I assumed that the 2 yr and 3 yr juvenile proportions (0.208, 0.792) as well as the 3 yr juvenile and 3 yr adult proportions (0.926, 0.074), as determined for the 1984 and 1985 winter samples (Table 4), also applied in 1985–86. This allowed derivation of the two total columns of Table 5 by solving \( x/(0.544 - x) = 0.208/0.792 \) and \( y/0.4310 = 0.074/0.926 \), with the total for 4 yr and older adults determined by subtraction. The body of the table was completed by multiplying the age-class totals by the appropriate proportions of male (0.507) and female (0.493) juveniles and male (0.632) and female (0.368) adults, determined for the 1985–86 samples. This procedure led to a slight difference (2.5%) in adult frequencies from those derived by using the adult 3 and 4 yr proportions (0.050, 0.950) calculated from the values in Table 4. The first method was preferred because it incorporated the assumption of 0.0741 metamorphosis of 1 yr larvae into the derivation of frequencies of later years.

Since an estimate of female survivorship was needed, I used the ratio of frequencies of 3 yr (juveniles plus adults) and 4 yr and older (adults only) females from Table 5, equal to \( \frac{0.2250}{0.1553} = 1.449 \), to iteratively calculate a constant annual survivorship value which yielded this ratio. That is, the iteration began with the proportion of 3 yr females, and determined for a given number of generations a constant annual survivorship coefficient yielding frequencies which summed to the estimated proportion of 4 yr and older females. This value, determined for 10 generations, was 0.408. The number of generations selected for the iteration, beyond two, has little effect on the result.

Fecundity.—I estimated fecundity from counts of yolked oocytes in the ovaries of 16 gravid females. The values ranged from 28–56 (\( x = 40.9, \text{SE} = 2.19 \)). Egg number increased approximately linearly with SVL. The least-squares regression equation was \( Y = -76.76 + 2.994X \), where \( Y = \text{oocyte number and } X = \text{SVL}. \) The regression coefficient differed significantly from 0 (\( F = 20.53, df = 1, 14, P < 0.001 \)). The regression equation was used to estimate age-specific fecundity in constructing the \( m_x \) column of the life table, as described below.
Table 6. Calculation of Age-specific Snout-Vent Lengths for Females of Eurycea wilderae at Station Creek. The cumulative percentages of SVL are derived from the last three 1985–86 samples, and the cumulative percentages of age are determined from age 4, based on the estimate of 0.408 annual survivorship. The percent by age values are interpolated into the percent by size column to yield estimates of SVL at each age by interpolation, given in the last column.

<table>
<thead>
<tr>
<th>SVL (mm)</th>
<th>N</th>
<th>Cumulative values</th>
<th>Age (yr)</th>
<th>Cumulative to this age</th>
<th>SVL at this age</th>
</tr>
</thead>
<tbody>
<tr>
<td>36</td>
<td>3</td>
<td>3</td>
<td>7.14</td>
<td></td>
<td></td>
</tr>
<tr>
<td>37</td>
<td>7</td>
<td>10</td>
<td>23.81</td>
<td></td>
<td></td>
</tr>
<tr>
<td>38</td>
<td>4</td>
<td>14</td>
<td>33.33</td>
<td></td>
<td></td>
</tr>
<tr>
<td>39</td>
<td>5</td>
<td>19</td>
<td>45.24</td>
<td></td>
<td></td>
</tr>
<tr>
<td>40</td>
<td>9</td>
<td>28</td>
<td>66.67</td>
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</tr>
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<td>41</td>
<td>9</td>
<td>37</td>
<td>88.10</td>
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</tr>
<tr>
<td>42</td>
<td>4</td>
<td>41</td>
<td>97.62</td>
<td></td>
<td></td>
</tr>
<tr>
<td>43</td>
<td>1</td>
<td>42</td>
<td>100</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Age-specific female size.—In order to develop the m, column of the life table it was necessary to determine the body size of mature females at each age of life, inasmuch as fecundity increases with size. Hairston’s (1983) procedure was followed. The first step was to calculate cumulative percentages of females according to age, based on the estimated value of 0.408 for constant adult female annual survivorship. I used age 4 for the starting value, ignoring the small proportion of females which mature at age 3. The calculation was continued until the proportion fell below 0.001, and the values were then incorporated into Table 6.

The next step was to calculate cumulative frequencies of mature females by size, based on the SVL data in the last three fall-winter samples of 1985–86. The cumulative percentages-by-size were combined with the cumulative percentages-by-age in Table 6, in order to interpolate estimated SVLs for ages 4–10, as shown in the last column of the table.

Completion of a life table.—Once estimates of body size at each age of life were available, it was possible to compute an m, column, representing female eggs/female at age x. Assuming equal numbers of male and female eggs and an annual female reproductive schedule, the m, values were obtained by substituting the SVL for each age (last column of Table 6) into the regression equation derived earlier, Y = −76.76 + 2.994X. The result was halved, since what was required was an estimate of female eggs. For the small proportion of adult 3 yr females, I used the smallest recorded SVL of mature females (36 mm), calculated egg number from the regression equation, halved the result, and multiplied this value by 0.0564, which is the estimated proportion of mature adults among all 3 yr females.

Combining the m, values so derived with the l, estimates obtained earlier allowed calculation of I,m, values and completion of the life table (Table 7). The sum of the I,m, column yielded a value of R0, or the female replacement rate, equal to 0.821. This is lower than the required R0 of 1.0 based on the assumption of a stable age distribution and r = 0.

It is possible that E. wilderae is like D. ochrophaeus, where growth ceases at maturation (Tilly, 1980). This would mean that the observed variation in adult female body size was the result of variation in larval and juvenile growth rates, such that mature females of different ages would have the same mean body size and probably the same mean clutch size. Recalculating the life table on this basis, using m, = 20.5 female eggs/female, which is half the mean count of yolked eggs in 16 gravid females, yields a slightly lower value (R0 = 0.785) for the net reproductive rate than calculated above.

The methods followed in constructing the life table have assumed a stable age distribution and a population growth rate, r, of 0. A consequence of these assumptions is that R0 = 1.0, since in
a stable, stationary population, each female is expected to just replace herself. Thus the calculations of \( R_0 = 0.821 \) or 0.785 imply errors in sampling and/or violations of the assumptions followed in the sequence of calculations.

An alternative procedure advocated by Michod and Anderson (1980) is to make no assumption concerning \( r \) and to calculate the life table and \( r \) jointly from age-class frequencies and fecundities, assuming a stable age distribution. Using the estimated age-class frequencies and assuming a constant ratio of metamorphosed females in successive age classes, the finite rate of increase, \( \lambda \), which is related to \( r \) through \( r = \ln \lambda \), can be calculated by the formula given by Michod and Anderson,

\[
\lambda = \sum_{i=0}^{n-1} \frac{N_i(t)}{N_0(t)} l_i m_i,
\]

where \( N_i(t) \) = number in age class \( i \) at time \( t \), \( N_0(t) \) = number in the 0th age class at time \( t \), \( l_i \) = survivorship into 0th age class of newborns, and \( m_i \) = average fecundity of females in age class \( i \). In the present study, \( l_0 = 1.0 \), since the sampling period coincided with egg-laying. If the \( l_i \) column of Table 7 is considered a table of age-class proportions, \( N_i(t) \), where the proportions are constant for adult females, then calculation of \( \lambda \) yields \( \lambda = 0.821 \) and \( r = -0.197 \), which indicates a declining population. The \( l_i \) table (not shown) generated by the procedure has lower values than those calculated on the assumption of \( r = 0 \). The values can be used to derive an estimate of mean generation time using

\[
G = \frac{\sum x l_i m_i}{\sum l_i m_i},
\]

which for the study population was 4.4 yr.

**Discussion**

The derivation of a calculated value of \( R_0 \) below 1.0 suggests a combination of sampling and interpretive errors in estimating age specific survivorship and fecundity of *E. wilderae*. The fecundity or \( m_i \) values, though based on ovarian egg counts, were probably reliable. Dissections of spent females collected after oviposition revealed no residual ova in the ovaries. Apparently all of the yolked oocytes are ordinarily deposited. Although there may be compounded errors arising from the complex method of determining age-specific clutch sizes, the SVL range of mature females was so narrow that this source of error was probably negligible.

The accuracy of the \( l_i \) values is more questionable. Aside from the uncertainties involved in estimating survivorship to maturity by converting frequencies of life-history stages to age-class frequencies, the difference in adult male and female survivorship raises questions. Since mature females oviposit on an annual schedule, which involves carrying a complement of yolked oocytes through the autumn and winter and then attending the eggs until hatching in late spring, this heavy reproductive demand may lower female survivorship relative to that of males. Alternatively, gravid females may be more secretive than males and juveniles of either sex in the winter months, as they gather in concealed sites in preparation for oviposition. In this case, the calculation of low female survivorship was a sampling error, since the calculation relied on an unbiased estimate of juvenile and adult frequencies. Perhaps both factors contributed to the low calculated value of female survivorship.

The two male morphs found in *E. wilderae* at Station Creek correspond to those described by Sever (1979) for several populations of this species in the southern Blue Ridge. Reagan (1984) has reported variation in courtship behavior between morphs. Since at Station Creek the cirrigerous males (Sever's *wilderae*) tended to be smaller than the non-cirrigerous males (Sever's morph A), it is possible that the variation is ontogenetic, and is related to shifts in courtship behavior with age. Jacobs (1987) was unable to detect genetic differences between these morphs.

In comparing the life table of *E. wilderae* with others, Organ's (1961) life tables for five species of *Desmognathus* were based on the interpretation that all five had the same age at first reproduction (5 yr, females), and he calculated essentially the same mean generation time for them (5.1-5.6 yr). More recent studies on *D. ochrophaeus* (Tilley, 1973, 1974, 1980) and *D. fuscus* (Spight, 1967; Danstedt, 1975; Jones, 1986) cast doubt on the generality of Organ's findings, and suggest a need for additional comparative studies in this genus. For the species of southern Appalachian plethodontids for which more recent life tables have been constructed, *E. wilderae* shows lower mean generation time, lower survivorship and higher fe-
fecundity than either *D. ochrophaeus* (Tilley, 1980) or *P. jordani* (Hairston, 1983).

In *D. ochrophaeus*, where females are somewhat smaller than those of *E. wilderae*, m$_x$ values are considerably lower. Tilley (1980) derived m$_x$ columns for *D. ochrophaeus* based on his findings that clutch size does not increase with growth after attainment of sexual maturity and that females reproduce annually. He calculated m$_x$ as half the average clutch size, estimating clutch size from counts of yolked oocytes in live gravid females. For each of two study populations he used a constant m$_x$ value over the age range of mature females. Tilley estimated mean generation times of 5.6 and 7.5 yr for the two populations he studied.

For *P. jordani* Hairston (1983) obtained an independent estimate of a stable population (r = 0), and was then able to estimate survivorship for each age from the size-frequency data. However, he had no direct estimate for 1st yr survival, and estimated this value indirectly on the basis of r = 0. This yielded a set of annual survival values of 0.837, 0.364, and 0.484 for the first 3 yr followed by an estimate of 0.81 for each year thereafter. The high survival value for the 1st yr relative to the two succeeding years seems too high, even assuming parental care for the entire period. Ovarian egg counts in this species are only \( \frac{1}{4} to \frac{1}{2} \) those of the smaller *E. wilderae*, and the m$_x$ values are further reduced because females do not reproduce annually and because not all yolked eggs are oviposited. Hairston used dissection data in determining fecundity, but multiplied derived clutch sizes by a factor of 0.582 to estimate m$_x$ values. This factor was chosen on the basis of Highton's (1956) findings on *P. glutinosus* in Florida that field clutches of eggs are smaller than ovarian complements. However, Highton observed only five clutches in the field. Had Hairston not so reduced the m$_x$ estimate, the calculated l$_1$ would have been considerably lower (0.489). Yet this would have lowered mean generation time only slightly, from 9.8 to 9.5 yr.

*Eurycea wilderae*, *Desmognathus ochrophaeus*, and *Plethodon jordani* are the three species of southern Appalachian salamanders for which recent life tables have been derived. Despite considerable differences in habitats, larval period, body size, and various demographic parameters, all three have about the same age at first reproduction, 4 or 5 yr in *D. ochrophaeus* and 4 yr in both *E. wilderae* and *P. jordani*. This may be generally applicable in southern Appalachian plethodontids (Houck, 1977; Tilley, 1977). Thus, although survivorship may be higher in the more terrestrial species (e.g., as reflected in variation in mean generation time of the above three species), the evolutionary response of developmental features to changes in survival probabilities associated with adaptation to new habitats may have involved greater adjustments in fecundity schedules than in age at first reproduction. Since growth rates decline sharply after maturation in plethodontids (Tilley, 1980), shifts in age at first reproduction may be constrained by niche-specific body-size requirements. The relationship among growth, maturation, size, and age in the evolutionary diversification of plethodontids is an important unresolved question in these salamanders.

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**Literature Cited**


Effect of Temperature Acclimation on Locomotory Performance Curves in the Toad,

Bufo woodhousii woodhousii

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Four indices of burst locomotion in Woodhouse's toad, Bufo woodhousii woodhousii were measured in the laboratory. The toads were acclimated at 20°C or 30°C and were tested at 5°C intervals from 15-30°C. Acclimation temperature had a significant effect on all four indices of locomotion, but the effect differed with different indices and with test temperature. Mean velocity was greater at higher test temperatures regardless of acclimation temperature. Mean jump frequency was greater for 20°C than 30°C-acclimated toads. Mean and longest jump lengths were greater for 30°C-acclimated animals. However, these two measures of jump length showed different patterns of thermal sensitivity depending on acclimation temperature. These differences between indices suggest that one should be cautious in making comparisons, both within and between species, of temperature effects on locomotory performance in amphibians.

LOCOMOTORY performance can potentially affect an animal’s success in prey capture, predator avoidance, and mating (Bartholomew, 1977; Huey and Stevenson, 1979). In ectotherms, locomotory performance varies unimodally with body temperatures; fitted curves have peaks that represent an optimal range of performance and tails that reflect the