METABOLIC GROWTH DRIVES PACE-OF-LIFE IN Plethodontid Salamanders: Effects in Dusky Salamanders (*Desmognathus*) and Woodland Salamanders (*Plethodon*)

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Abstract.—I applied a metabolic growth model in several species of salamanders of the genera *Desmognathus* and *Plethodon* to test the efficacy of the metabolic growth equation of West et al. (2001). The metabolic growth equation is derived from basic principles of cellular energetics and is more realistic than traditional goodness-of-fit growth models. I used data from published sources on populations in the southern Blue Ridge Mountains of North Carolina, USA. Metabolic growth coefficients generated by the data demonstrated that these salamanders have extremely low growth rates in comparison to those reported for other animals. I suggest that selection for low rates of cellular metabolism effected by genomic proliferation set plethodontids on a slow track of growth, development, reproduction, and longevity, which ostensibly promoted geographic expansion and diversification in morphology, life history, and ecology. I showed that the low growth parameters of the plethodontids in question have a close fit to a universal animal growth curve. In addition, evaluation of age at first reproduction in females and age equal to generation time demonstrated the expected scaling relationship with body mass, wherein these landmark ages are proportional to mass^{1/4}. I discuss plethodontid life histories under the premise that pace-of-life in animals is set by generation time. Ecologically, the slow life histories of the salamanders I studied define the role of these (and other) plethodontids in the forest ecosystems of the southern Appalachian Mountains.

Key Words.-age; Amphibia; body size; Caudata; generation time; life history

INTRODUCTION

The life histories of many animals conform to a fast-slow pace-of-life continuum that incorporates such traits as growth and development (fast-slow), number and size of offspring (many/small-few/ large), and generation time and longevity (shortlong; Healy et al. 2019; Brown et al. 2022). The extremes are represented by such animals as House Flies, Musca domestica (fast) and Blue Whale, Balaenoptera musculus (slow; Wright et al. 2020). Nevertheless, disparities occur, particularly involving growth and developmental rates and longevity versus reproductive rates and offspring number and size, as in organisms like mayflies and butterflies vis-à-vis oak trees and sharks (see figure 4 in Wright et al. 2020). The pace-of-life concept is often referred to as the pace-of-life-syndrome or POLS (e.g., Milles et al. 2022). In addition to the rate attributes noted above, the pace-of-life syndrome also involves those behavioral and personality traits that influence the life history and demography of populations (Réale et al. 2010; Vasilieva 2022).

Of the 824 species of salamanders in the world, nearly 2/3 are members of the family of lungless salamanders, the Plethodontidae (https:// amphibiaweb.org). Here I have re-assessed growth phenomena of several species of plethodontids of the genera Desmognathus and Plethodon to test the efficacy of the metabolic growth model of West et al. (2001) in comparative studies of animal life histories. These and other plethodontids lie at the slow end of the pace-of-life gradient of life histories observed in extant vertebrates of similar body size, which is reflected by such traits as growth and development, generation time, and reproductive rate, as well as behavioral traits that prescribe low activity levels (Woodley 2017; Bruce 2023). The slow track of the pace-of-life syndrome applies to representatives of all three life-history modes found in the family, i.e., paedomorphosis, metamorphosis, and direct development (Bonett 2016; Beachy et al. 2017). The slow life histories of plethodontids are mediated by low metabolic rates (Feder 1983; Gifford 2016; Markle and Kozak 2018), which reflect the large cell sizes, large genome sizes, and longer cell cycles of

these salamanders (Sessions 2008).

In theory, slow life histories are associated with strong density-dependent selection, whereas fast life histories are expected in species experiencing density-independent selection (Wright et al. 2020; Milles et al. 2022). As noted by Wright et al. (2020) species with complex life cycles may evolve differential survival and reproductive strategies along the fast–slow continuum in response to variation in the strength of density dependence among habitats utilized by different stages of the life cycle. All the species of plethodontids evaluated in my study, however, including metamorphosing and directdeveloping species, lie at the slow end of the pace-oflife syndrome (Bruce 2023).

The populations Desmognathus of and Plethodon I studied occur in the southern Blue Ridge Physiographic Province, in North Carolina, southeastern USA (Figs. 1, 2). The evaluations of growth were carried out within the prescripts of the metabolic model developed by West et al. (2001), which was based on application of cellular metabolic parameters at the organismal level. In animals the relationship of metabolic rate (P) to body mass (K) is expressed by the equation $P = \gamma K^{b}$, with the scaling factor (b) tending to vary around ³/₄ (Calder 1984; Schmidt-Nielsen 1984; Brown et al. 2022). Setting b = $\frac{3}{4}$ and dividing by mass yields an expression for the specific metabolic rate, $P^* = \gamma K^{-1/4}$. The reciprocal provides an equation for metabolic time, $t_{met} = (1/\gamma)$ K^{1/4}. For 16 species of plethodontid salamanders in the genera Desmognathus and Plethodon, Markle and Kozak (2018) reported that the effect of body mass on metabolic rate changes with temperature, with the scaling factor increasing from 0.59 at 5° C to 0.71 at both 15° and 25° C. The latter value, which is close to ³/₄, applies to temperatures reflecting typical levels of activity in plethodontids. In reference to the emphasis on thermal acclimation by the authors, they found that species with narrow geographic ranges have poorer acclimation ability than those with wider ranges.

My rationale for conducting a metabolic growth analysis was an interest in comparing growth rates of *Desmognathus* and *Plethodon* with those of other animals, as reported by West et al. (2001). I expected that plethodontids would tend to fall at the lower end of the range of growth parameters in animals, especially vertebrates. Secondly, I examined the position of these plethodontids on the universal animal growth curve that was generated by West et al. (2001). The goal was to examine the goodness-of-fit of the growth



FIGURE 1. General locations of the source populations of salamanders in southwestern North Carolina, USA: 1 - Wolf Creek; 2 - Southern Nantahala Mountains; 3 - Dry Falls; 4 - Whiteside Mountain; 5 - Brooks Branch; and 6 - Courthouse Creek. Insert is Courthouse Creek Valley, the location of the study by Hairston (1983) of the Southern Gray-cheeked Salamander (*Plethodon metcalfi*) and the Southern Appalachian Salamander (*Plethodon teyahalee*). (Photographed by Richard C. Bruce).

analyses to the universal growth curve. Additionally, I determined the relationship between metabolic timing and body mass in reference to the timing of initial reproduction in females and generation time. I expected that timing of these landmark ages would vary according to the 1/4th power of mass. Finally, I discuss the ramifications of the growth analysis to the ecological role of these and other plethodontids in the ecosystems of the southern Appalachian Mountains of the U.S.

MATERIALS AND METHODS

The database.---I evaluated published data from sources dealing with life histories and demographics of Desmognathus (Tilley 1980; Bruce 2017, 2021, 2022, 2024), and the Southern Gray-cheeked Salamander (Plethodon metcalfi; Hairston 1983; Ash et al. 2003). They included studies of the life histories and demographics of six species of Desmognathus in two assemblages: Nantahala Black-bellied Salamanders (D. amphileucus), Seal Salamanders (D. monticola), Ocoee Salamanders (D. ocoee), Seepage Salamanders (D. aeneus), and Southern Pygmy Salamanders (D. wrighti) in the southern Nantahala Mountains in Macon and Clay counties, North Carolina, USA; and D. amphileucus, D. monticola, and Tallulah Salamanders (D. perlapsus) in the Wolf Creek watershed on Cullowhee Mountain in the Cowee Mountains in Jackson County, North Carolina, USA (Bruce 2017, 2021, 2022, 2024). I also evaluated data of two populations of D. perlapsus in the Blue Ridge Mountains, referred to as Dry Falls in Macon County



FIGURE 2. (1) Southern Gray-cheeked Salamander (*Plethodon metcalfi*), Balsam Mountains, North Carolina. (2) Southern Appalachian Salamander (*Plethodon teyahalee*), Balsam Mountains. (3) Southern Red-backed Salamander (*Plethodon serratus*), Balsam Mountains. (4) Southern Pygmy Salamander (*Desmognathus wright*), (above); Seepage Salamander (*Desmognathus aeneus*), Nantahala Mountains, North Carolina, USA. (5) Nantahala Black-bellied Salamander (*Desmognathus amphileucus*), Nantahala Mountains. (6) Larva of *Desmognathus amphileucus*, Nantahala Mountains. (7) Seal Salamander (*Desmognathus monticola*), Nantahala Mountains. (8) Ocoee Salamander (*Desmognathus ocoee*), Nantahala Mountains. (9) Tallulah Salamander (*Desmognathus perlapsus*), Wolf Creek, North Carolina, USA. Photographs are not to scale. (Photographed by Richard C. Bruce).

and Whiteside Mountain in Jackson County (Tilley 1980); and two populations of *Plethodon metcalfi*, one in the Courthouse Creek watershed in the Balsam Mountains of Transylvania County (Hairston, 1983), the other in the Blue Ridge Mountains in the Brooks Branch watershed near Highlands in Macon County (Ash et al. 2003). Hairston (1983) also included the Southern Appalachian Salamander (*Plethodon teyahalee*) in his study at Courthouse Creek but provided less detail than for *P. metcalfi*. The former species occurred also at Brooks Branch. A third species of *Plethodon*, the Southern Red-backed Salamander (*P. serratus*), was observed infrequently at both localities (Hairston 1981; Ash 1997). Specific locality data were provided in the source publications.

With the exception of the Brooks Branch population of *P. metcalfi* (Ash et al. 2003), life tables were derived for each population. The life tables were based on the female component of each

population and included estimates of age, body size, survival, fecundity, and generation time. The authors who derived the life tables assumed that populations were in stable equilibria during the period when their field studies were conducted. Such an equilibrium is known as an attractor and originates from conditions over the long term that birth rate = death rate, intrinsic growth rate (r) = 0, and net reproductive rate (R_0) = 1.0 (Vandermeer and Goldberg 2013).

In three of the earlier studies of *Desmognathus*, I fitted Gompertz growth functions to skeletochronological estimates of snout-to-vent lengths (= standard length, SL; Bruce 2017, 2021, 2022). These analyses generated estimates of asymptotic sizes (SL_{∞}). I assumed that the latter were close to the maxima expected for these populations in field samples. I converted all of the SL data from the above studies to dry body mass, and I have done the same for Dry Falls and Whiteside populations of *D. perlapsus* (Tilley 1980), Courthouse Creek and Brooks Branch populations of *P. metcalfi* (Hairston 1983; Ash et al. 2003), and the Nantahala populations of *D. aeneus* and *D. wrighti* (Bruce 2024).

The required data I used were reliable estimates of age (x, in days) and body mass (g), including size at hatching, maximum size (approximately asymptotic size), and a range of intermediate values of size. The size metric I used is dry body mass (K), derived from estimates of live body mass (wet weight, W) according to K = 0.3125W (Burger et al. 2021). Regressions of W (g) on live standard length (SL in mm) in the source species of *Desmognathus* were provided in Bruce (2018, 2024).

To convert standard lengths to the required body mass estimates of *P. metcalfi* I used the length-tomass regression of the Brooks Branch population of *P. metcalfi* (Ash et al. 2003). The latter authors provided a plot of ln mass on ln SL (their figure 2) but omitted the equation, which is ln W = $-10.18 + 2.794 \times \ln SL$, $r^2 = 0.885$. The equation for a small sample (n = 14) of the Balsam Mountain population of *P. metcalfi* is nearly identical, ln W = $-10.08 + 2.777 \times \ln SL$, $r^2 = 0.950$; unpubl. data).

Metabolic growth.—Given that the life tables in the source publications were based on females, the metabolic growth curves in the current study were derived from the female data of those sources. For example, in my studies of Nantahala and Wolf Creek desmognathans, what I called the female dataset comprised larvae and small juveniles for which I could not determine sex, larger female juveniles, and sexually mature females (Bruce 2017, 2021, 2022, 2024). Although other authors used different procedures, all the life tables were female based, as were the estimates of K_0 , K_x , and K_∞ that were required to estimate the growth coefficient, *a*.

For each population of *Desmognathus* and *Plethodon* I fitted the values of dry body mass (K) and age in days (x) to the growth equation of West et al. (2001: their fig. 5), which is expressed herein as

$$K_{x} = K_{\infty} \cdot (1 - (1 - (K_{0}/K_{\infty})^{1/4}) \cdot (\exp(-a \cdot x/4 \cdot K_{\infty}^{-1/4})))^{4}$$
(1)

where $K_0 = body$ mass at hatching and $K_{\infty} = asymptotic body mass. A growth coefficient,$ *a* $, formulated in units of grams dry biomass/day, was calculated from estimates of <math>K_0$, K_{∞} , and a known intermediate value of K_x in the source publications. The full derivation of the metabolic growth model is provided in the Appendix.

Universal animal growth curve—West et al. (2001) formulated a dimensionless universal animal growth curve, based on the negative exponential growth model, $K_x = K_{\infty} \cdot (1 - \exp(-\beta \cdot x))$ (Panik 2014), and expressed by West et al. as

$$r = 1 - \exp(-\tau) \tag{2}$$

in which r = the dimensionless size ratio, $(K_x/K_{\infty})^{1/4}$, and $\tau =$ the dimensionless time variable, $(a \cdot x/4 \cdot K_{\infty}^{-1/4}) - \ln(1 - (K_0/K_{\infty})^{1/4})$. Thus, equation (2) can be written as

$$(K_{x}/K_{\infty})^{1/4} = 1 - (1 - (K_{0}/K_{\infty})^{1/4}) \cdot (\exp(-a/4 \cdot K_{\infty}^{1/4}))^{x} (3)$$

I fitted a range of values to this growth curve that were calculated from unbiased subsets of estimates of age and the corresponding body size in the samples of the six populations of Nantahala and Wolf Creek *Desmognathus* for which I used skeletochronology to determine age (Bruce 2017, 2021, 2022). For each sample, I included 12–15 individuals in the analysis.

Physiological timing and statistical analyses.— To examine the effects of body mass on timing (t_{max}) of selected life-history parameters, I examined body mass at age of first reproduction in females (x*) and age equal to generation time (G) by fitting log –log least-squares regression equations to $t_{met} = (1/\gamma)K_x^{b}$ in samples of the eight populations of Desmognathus at the Nantahala and Wolf Creek localities. The estimates of x* and G were generated in the source publications independently of the metabolic growth model derived in this study. The predicted slope (b) or scaling exponent in each analysis was 1/4. I used Systat v13.2 (Grafiti, LLC, Palo Alto, California, USA) to analyze data. I verified mathematical computations with Mathematica13.1 (Wolfram Mathematica, Boston, Massachusetts, USA).

RESULTS

Estimated parameters of the metabolic growth model reflect the slow pace of life of these salamanders (Tables 1, 2). Growth curves generated by the model were sigmoidal, with the inflexion typically in the juvenile phase or during sexual maturation (Fig. 3). Data on variation in growth were provided in the source publications. Within each population the value of the growth coefficient (*a*) varied slightly according to the values of x and K_x that were incorporated into its calculation (see Appendix). The estimate, however,

was precise to the third decimal place: 0.002, 0.003, or 0.004 in each population. Within species (e.g., *D. amphileucus*, *D. monticola*, *D. perlapsus*, *P. metcalfi*), populations having larger body size tended to have a higher growth rate; however, there was no obvious correlation between body size and growth rate in the total dataset (Table 1). It is noteworthy that growth coefficients were especially high in the small species, *D. perlapsus*, with the larger woodland form at Wolf Creek having a higher growth rate than the smaller rock-face inhabitants at Dry Falls and Whiteside.

In *Plethodon metcalfi* the difference in *a* between the Brooks Branch and Courthouse Creek populations was extreme, and it was especially low at Courthouse Creek (0.00209). The inflexion of the growth curve was poorly defined in Courthouse Creek *P. metcalfi* and occurred later in the life cycle, following sexual maturation. Differences between the two *P. metcalfi* populations included smaller female body size at first reproduction (= 4 y in both populations) and smaller maximum size at Courthouse Creek (Tables 1, 2). The smaller sample of *P. teyahalee* at Courthouse Creek (Hairston 1983) did not allow derivation of a life table. He estimated that age at first reproduction in females of the larger *P. teyahalee* was 5 y, and that annual survival of the latter species (= 0.499) was similar to that of *P. metcalfi* (= 0.484). He later estimated generation time in *P. teyahalee* as \geq 10 y (Hairston 1987).

The dimensionless growth curve (Fig. 4) fitted to the Wolf Creek and Nantahala desmognathan data was essentially identical to the universal animal growth curve in West et al. (2001: their Fig. 2). Estimates of physiological times ($t_{met} = (1/\gamma)K^b$) based on age in days for the Wolf Creek and Nantahala *Desmognathus* (i.e., the only populations analyzed directly by this author) are generation time, G = 2477 ·K_{0.2388}, r^2 = 0.975, and age at first reproduction in females, x* = 2154 ·K^{0.2541}, r^2 = 0.971. The scaling coefficients are equal or close to the predicted value of 0.25. The plots of the log-transformed equations show tight fits of the data to the regression lines (Fig. 5).

TABLE 1. Application of the metabolic growth curve in species of *Desmognathus* and the Southern Gray-cheeked Salamander (*Plethodon metcalfi*), according to the equation $K_x = K_x(1 - (1 - (K_0/K_x)^{1/4})(\exp(-a \cdot x/4 \cdot K_x)^{1/4})))^4$. Unit of K is dry body mass (g). Parameters $K_0 = dry$ mass at hatching, $K_x = asymptotic dry mass$, a = growth coefficient, and K_i and x_i are dry mass and age in days at inflexion of the growth curve.

Locality/Species	K _∞	K ₀	а	K	X
Nantahala					
Nantahala Black-bellied Salamander, D. amphileucus	5.874	0.01620	0.00366	1.8588	1,916
Seal Salamander, D. monticola	2.694	0.01019	0.00392	0.8527	1,440
Ocoee Salamander, D. ocoee	0.662	0.00469	0.00327	0.2095	1,152
Seepage Salamander, D. aeneus	0.141	0.00201	0.00350	0.0446	674
Southern Pygmy Salamander, D. wrighti	0.109	0.00199	0.00304	0.0345	702
Wolf Creek					
Nantahala Black-bellied Salamander, D. amphileucus	5.372	0.01820	0.00342	1.7000	1,977
Seal Salamander, D. monticola	2.334	0.01187	0.00378	0.7388	1,407
Tallulah Salamander, D. perlapsus	0.445	0.00622	0.00419	0.1409	753
Dry Falls					
Tallulah Salamander, D. perlapsus	0.184	0.00622	0.00388	0.0584	559
Whiteside					
Tallulah Salamander, D. perlapsus	0.236	0.00622	0.00378	0.0748	643
Courthouse Creek					
Southern Gray-cheeked Salamander, P. metcalfi	1.430	0.01905	0.00209	0.4524	2,042
Brooks Branch					
Southern Gray-cheeked Salamander, P. metcalfi	2.448	0.03234	0.00394	0.7746	1,235

	Initial reproduction in females		Generation Time	
Locality / Species	Age (days)	Dry mass,K (g)	Age (days)	Dry mass, K (g)
Nantahala				
Nantahala Black-bellied Salamander, D. amphileucus	3,287	3.658	3,725	4.093
Seal Salamander, D. monticola	2,191	1.364	2,984	1.958
Ocoee Salamander, D. ocoee	1,461	0.287	2,586	0.499
Seepage Salamander, D. aeneus	1,096	0.078	1,457	0.100
Southern Pygmy Salamander, D. wrighti	1,096	0.057	1,435	0.073
Wolf Creek				
Nantahala Black-bellied Salamander, D. amphileucus	2,739	2.538	3,142	3.076
Seal Salamander, D. monticola	2,009	1.088	2,724	1.593
Tallulah Salamander, D. perlapsus	1,461	0.291	2,586	0.404
Dry Falls				
Tallulah Salamander, D. perlapsus	1,461	0.141	2,045	0.165
Whiteside				
Tallulah Salamander, D. perlapsus	1,826	0.182	2,739	0.218
Courthouse Creek				
Southern Gray-cheeked Salamander, P. metcalfi	1,461	0.290	3,575	0.859
Brooks Branch				
Southern Gray-cheeked Salamander, P. metcalfi	1,461	0.957		

TABLE 2. Age and size at life-history landmarks in species of *Desmognathus* and the Southern Gray-cheeked Salamander (*Plethodon metcalfi*). Lack of a life table precluded estimation of generation time for *P. metcalfi* at Brooks Branch.

DISCUSSION

Salamanders are characterized by the largest genomes of any comparable tetrapod taxon, and only lungfishes (Dipnoi) have larger genomes among vertebrates generally (Sessions 2008; Schartl et al. 2024). Among plethodontids the smallest genomes occur in Desmognathus (C-values approximately 15), whereas the C-values in *Plethodon* are greater (= 38.3 in Plethodon metcalfi; Hally et al. 1986; Sessions and Larson 1987; Itgen et al. 2022). Genome size is correlated with cell volume, length of the cell cycle, and tissue structure (Sessions 2008; Itgen et al. 2022). Given that the growth parameter of the metabolic growth equation employed herein is derived from cellular energetics in units of grams of cell mass/day, it is expected that animals with larger genomes and larger cells, such as salamanders generally and plethodontids specifically, have lower metabolic rates, lower growth and developmental rates, and lengthier generation times than other vertebrate animals of similar body size. These effects may be accentuated in the plethodontid salamanders, which are constrained by the limitations of buccopharyngeal and cutaneous respiration on metabolic rate and water balance (Feder 1983; Gifford 2016; Staub 2016; Beachy et al. 2017).

Under such constraints the evolution of lunglessness generated a low-key plethodontid niche that promoted the adaptive radiation of these salamanders in a variety of habitats in the North Temperate and Neotropical regions (Wake 1987; Petranka 1998; Ambrogio and Mezzadri 2017; Raffaëlli 2022). As noted by these authors, such a niche incorporates the relatively sedentary and secretive lifeways of plethodontids (shared with virtually all other salamanders), whereby the salamanders spend the daylight hours in concealment: under rocks in streams, under cover objects or in burrows in forests, in crevices in rock faces, or hidden in bromeliads and mosses in arboreal habitats, and emerge after dark to forage or to court The cavernicolous species, including and mate. metamorphosing and paedomorphic forms, spend all or part of their lives in cool, dark, subterranean



FIGURE 3. Plots of metabolic growth curves of six species of Dusky Salamanders (*Desmognathus*) and the Southern Gray-cheeked Salamander (*Plethodon metcalfi*) based on parameters listed in Table 1. Abbreviations of locations are Nant = Nantahala Mountains, WC = Wolf Creek = WS, Whiteside Mountain.; DF = Dry Falls; BB = Brooks Branch; CC = Courthouse Creek.

environs.

Metabolic growth parameters (a)in the plethodontids under consideration are much lower than those of the 13 animal species evaluated by West et al. (2001). These authors reported the highest values in endothermic birds and mammals, ranging from 0.21 to 1.47, the lowest in ectothermic fish (0.017-0.10) and the single invertebrate (shrimp, 0.027) evaluated. Among mammals the highest value (0.83) occurred in a shrew, but otherwise there was no trend associated with body size, ranging in five species from 0.21 to 0.36. All of the 13 listed species had higher values of a than the plethodontids that I evaluated (0.002-0.004). The differences reflect the slow pace of life and relatively sedentary behaviors of these salamanders. They do conform in their growth

attributes, however, to the universal animal growth curve formulated by West et al. (2001).

The metabolic growth curves were based on females, given that the life tables in the source publications were female oriented. The inflexions of the metabolic growth curves (x_i) tended to occur in the juvenile phase or later, during sexual maturation, prior to the age at initial reproduction. For the population of *P. metcalfi* at Courthouse Creek, however, the inflexion is later, post-maturational, and is ill-defined on the growth curve. This may reflect the lengthy life span (30 y or 10,958 d) and long generation time (9.8 y or 3,579 d) versus age at initial reproduction in females (4 y or 1,461 d), as derived in the life table in Hairston (1983). Terminating the life table at an earlier age (e.g., 16 y) and readjusting



FIGURE 4. The universal animal growth curve (equation 3 in the text) fitted to Nantahala and Wolf Creek Dusky salamanders (*Desmognathus*) where age was determined by skeletochronology. Each of the six populations is represented by 12–15 individuals of age (x) and dry body mass (K_x) that were selected arbitrarily from the larger samples.

survival (l_x) values to retain a net reproductive rate (R_0) of 1.0 yields an earlier and more realistic estimate of generation time (7.01 y). In a sample of 109 *P. metcalfi* at Brooks Branch, the oldest individual was 10 y using skeletochronology to determine age (Ash et al. 2003).

Brown et al. (2022) postulated that the pace of life is set by generation time (G) and that G scales as mass^{1/4}. They identified the four in the denominator of body-mass scaling factors as the biological time dimension. In the Nantahala and Wolf Creek desmognathans, the timing of generation length as well as age at first reproduction show the expected scaling of body mass according to $K^{1/4}$ as does the formulation of the metabolic growth parameter, *a*. These are key metrics in quantifying pace of life in the species of *Desmognathus* and *Plethodon* under study. Such relationships may apply to plethodontid salamanders generally, given their relatively small body sizes and lengthy life spans (Hairston 1987; Staub 2016; Lunghi 2022).

The species of Desmognathus and Plethodon that I studied are members of larger assemblages of plethodontid (and other) salamanders in the southern Blue Ridge Mountains. For example, I have encountered 12 species of plethodontids and four species of other families in the upper Nantahala River watershed (Fig. 1, locality 2). Similar assemblages occur throughout the region (e.g., Hairston 1987; Petranka et al. 1993; Hocking et al. 2020). It seems that plethodontids are the most important vertebrate predators in terrestrial food webs in these ecosystems (Hairston 1987; Petranka and Murray 2001; Davic and Welsh 2004) and play an even greater role in ecosystem energy flow than their counterparts in forest ecosystems in the northeastern U.S. (Burton and Likens 1975).

I suggest that the slow growth and developmental rates and lengthy life spans of plethodontids in the southern Blue Ridge convey stability in population numbers under density-dependent selection, which may contribute to stability in energy flux in these forest ecosystems generally. The authors of the source publications considered the populations they evaluated to be stable (i.e., $R_0 = 1.0$). In a loosely structured, long-term series of counts of four species



FIGURE 5. Plots of log-transformed metabolic-timing equations in the form $\ln(t_{met}) = \ln(1/\gamma) + b \cdot \ln(K)$, for t_{met} = generation time (G) and age at first reproduction in females (x*). LCL and UCL = lower and upper confidence limits, respectively, and LPL and UPL = lower and upper prediction limits, respectively. These plots are based on the eight populations of Nantahala and Wolf Creek Dusky salamanders (*Desmognathus*).

of Desmognathus in the southern Nantahalas conducted from 1972 through 1993, Hairston and Wiley (1993) and Hairston (1996) reported no trend in population numbers, up or down. The surveys were extended through 2007 with similar results, but they were analyzed more critically by Dixon and Pechmann (2005) and Warren and Bradford (2010). These surveys overlapped my demographic studies of these (and other) species of desmognathans in the southern Nantahalas and at Wolf Creek, in which I necessarily assumed fluctuations in population numbers around a point attractor (e.g., Bruce 2021). Nevertheless, recent assessments of amphibian declines at the global level (Luedtke et al. 2023; Nowakoski et al. 2023) underscore several decades of concerns of the viability of species and communities of salamanders in the southern Blue Ridge (e.g., Petranka et al. 1993; Ash et al. 2003; Milanovich et al. 2010; Hocking et al. 2020; DiRenzo et al. 2021). The results of such studies (and others), which have identified detrimental effects of habitat loss, climate change, and disease, justify continued monitoring of population status and community organization of plethodontids in the region.

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RICHARD C. BRUCE is a Professor Emeritus of Biology at Western Carolina University in Cullowhee, North Carolina, USA, where he taught for 39 y. For 27 of those years, he also served as Director of Highlands Biological Station in Highlands, North Carolina, USA. He earned a B.S. in Biology at Tufts University, Medford, Massachusetts, USA, and a M.A. and Ph.D. from Duke University, Durham, North Carolina, USA. He also studied at the Mt. Desert Island Biological Laboratory and Duke University Marine Laboratory. Rich is a vertebrate zoologist with a special interest in the ecology, demography, and life histories of plethodontid salamanders. His research has focused on salamanders of the southern Blue Ridge Mountains, beginning with his dissertation research on a comparative study of the life histories of the two species of *Pseudotriton*, conducted at Duke under the mentorship of Joseph Bailey. His later studies, especially those on *Desmognathus*, benefitted from a close association with Nelson G. Hairston, Sr. (Photographed by Elizabeth Bruce). Bruce.—Metabolic growth in Plethodontid salamanders.

APPENDIX

Metabolic Growth Model

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The growth parameter (= a, in grams/day) formulated by West et al. (2001) was derived from energetic aspects of cellular metabolism, and applied to organismal growth as

$$dK_{y}/dx = a \cdot K_{x}^{3/4} \cdot (1 - (K_{y}/K_{\omega})^{1/4}),$$
(1)

where $K_x = dry body mass at age x in days and K_x = asymptotic dry body mass (West et al., 2001: equation 4). Integrating equation (1) yields a sigmoidal growth equation (West et al., 2001: equation 5), similar in form to Gompertz and von Bertalanffy growth equations. The integral of the West et al. equation is$

$$\frac{|1/(K_x^{3/4}(1-(K_x/K_x)^{1/4}))\cdot dK_x = |a \cdot dx, \text{ yielding})}{-4 \cdot K_x^{1/4} \cdot \ln((K_x^{1/4}-K_x^{1/4}) - |a \cdot x + \text{constant}.$$
(2)

When x = 0, the initial condition of the system, the constant = $-4 \cdot K_{\infty}^{-1/4} \cdot \ln((K_{\infty}^{-1/4} - K_{0}^{-1/4})/K_{\infty}^{-1/4})$. Then, dividing equation (2) by $-4 \cdot K_{\infty}^{-1/4}$ yields

.

$$\ln((K_{\infty}^{1/4} - K_{x}^{1/4})/(K_{\infty}^{1/4} - K_{0}^{1/4})) = -a \cdot x/4 \cdot K_{\infty}^{1/4}$$
(3)
and $a = -(\ln((K_{\infty}^{1/4} - K_{x}^{1/4})/(K_{\infty}^{1/4} - K_{0}^{1/4})))/(x/4 \cdot K_{\infty}^{1/4}).$ (4)

Equation (3) is equivalent to

$$K_{x} = K_{x} \cdot (1 - (1 - (K_{0}/K_{x})^{1/4}) \cdot (\exp(-a \cdot x/4 \cdot K_{x}^{-1/4})))^{4}.$$
(5)

And equation (5) is equal to equation (5) in West et al. (2001) raised to the power of 4. The first derivative of equation (5) is

$$dK_{x}/dx = 4K_{\infty} \cdot (1 - (1 - (K_{0}/K_{\infty})^{1/4}) \cdot exp(-a \cdot x/4 \cdot K_{\infty}^{-1/4}))^{3} \cdot (-(1 - (K_{0}/K_{\infty})^{1/4})) \cdot exp(-a \cdot x/4 \cdot K_{\infty}^{-1/4}) \cdot (-a/4 \cdot K_{\infty}^{-1/4}),$$

and the second derivative is

$$\frac{d^2K_y/dx^2 = 12 \cdot K_{\infty} \cdot (1 - (1 - (K_0/K_{\infty})^{1/4}) \cdot exp(-a \cdot x/4 \cdot K_{\infty}^{1/4})^{2} \cdot (-(1 - (K_0/K_{\infty})^{1/4}))^2 \cdot exp(-a \cdot x/4 \cdot K_{\infty}^{-1/4})^2 \cdot (-a/4 \cdot K_{\infty}^{-1/4})^2 + 4 \cdot K_{\infty} \cdot (1 - (1 - (K_0/K_{\infty})^{1/4}) \cdot exp(-a \cdot x/4 \cdot K_{\infty}^{-1/4})^{3} \cdot (-(1 - (K_0/K_{\infty})^{1/4})) \cdot exp(-a \cdot x/4 \cdot K_{\infty}^{-1/4})^2 \cdot (-a/4 \cdot K_{\infty}^{-1/4})^2 \cdot (-a$$

(6)

Setting $d^2K_1/dx^2 = 0$, representing the inflexion of the growth curve, and solving for x, the age at the inflexion, yields

$$\mathbf{x}_{i} = (\ln(4) + \ln(1 - (\mathbf{K}_{0}/\mathbf{K}_{\infty})^{1/4}))/(a/4 \cdot \mathbf{K}_{\infty}^{1/4}).$$

Application of equation (5) for the age at inflexion yields

 $K_i = (3/4)^4 \cdot K_{\infty}$.