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Size and Cycle in Dusky Salamanders

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Abstract.—**The equal fitness paradigm (EFP) is a life-history model in which the currency of fitness is usable energy rather than individuals, and the principal trade-off is between survival, evaluated as generation time, and productivity, evaluated as growth and reproductive rates. In the current study I examined variation in generation time, age at first reproduction, productivity, and mortality in salamanders of the genus *Desmognathus* within the framework of the EFP. *Desmognathus* salamanders are restricted to eastern North America, with a center of distribution in the southern Appalachian Mountains. The data sources of the present report are published studies of life histories and demographics of five species of *Desmognathus* that include the smallest and largest members of the genus. The analysis showed that *Desmognathus* salamanders have greater ages at first reproduction, lengthier generation times, lower productivities, and lower mortality rates than are predicted by the scaling functions of the EFP for vertebrates of equivalent sizes. The differences among species in these parameters are correlated with variation in adult body size and the association between body size and habitat utilization in the genus, wherein the largest species are aquatic in mountain streams and the smallest are terrestrial in mesic forests. Streamside species of intermediate size exploit a broader range of habitats and are more widely distributed than the stream- and forest-dwelling forms. It is likely that the streamside mode of life in *Desmognathus* represents an adaptation promoting dispersal. Adaptive radiation in the genus is expressed in extreme life-history and body-size diversification mediated through variation in age at first reproduction and generation time.**

Analysis of life-history strategies and testing of life-history theory remain challenging areas of study in evolutionary ecology, given the complexities of trade-off relationships among the many traits that constitute a "life history" in one or another group of organisms (Roff et al., 2006; Saeki et al., 2014; Dani and Kodandaramaiah, 2017; Healy et al., 2019). A large body of research has shown that life histories of many animals tend to sort along one or more fast–slow "pace-of-life" axes of variation involving trade-offs among traits associated with biological timing, like growth rate and generation time (e.g., Wright et al., 2020). A second axis of life-history variation has been termed the "shape-of-life" continuum, which pertains to distribution of mortality risk and the spread of reproduction, that is, semelparity versus iteroparity (Healy et al., 2019). The latter authors emphasized the roles of metabolic rate and energy expenditure in determining the position of a species on the fast–slow axis. However, the year before, Brown et al. (2018) had shifted the focus of life-history variation to energy entirely by describing trait variation in the currency of energy and formulating trade-off relationships in an equal fitness paradigm (EFP; Burger et al., 2021). Under the EFP the essential trade-off is between survival, expressed as generation time, and productivity, expressed as individual growth and reproduction of offspring. An objective of the present report is evaluation of life histories of *Desmognathus* salamanders in the framework of the EFP, given my contention of the importance of age at first reproduction (and by extension generation time) in driving diversification in body size and life history in these salamanders (Bruce, 2018, 2022).

The genus *Desmognathus* is a member of the Plethodontidae, the largest of the 11 families of salamanders, having over 60% of the world's more than 780 salamander species (AmphibiaWeb, 2022). Plethodontids are lungless, and exchange gases through a moist skin and mouth lining. As a consequence plethodontids have low metabolic rates, low growth rates, and relatively sedentary lifestyles in moist habitats (Feder, 1983; Gatten et al., 1992; Gifford, 2016). Nevertheless, they are the most speciose and ecologically diverse group of extant salamanders and are widely distributed in the North Temperate and Neotropical zones of the Americas, with a few localized representatives in the Old World (Kozak, 2017; Wake, 2017). Plethodontids are adapted to a broad range of aquatic, subterranean, terrestrial, and arboreal habitats, and are often numerically abundant (Wells, 2007). Life cycles include paedomorphosis, metamorphosis, and direct development (Beachy et al., 2017).

Desmognathus is a complex taxon comprising 30 named species and many candidate species that are found from sea level to the summits of the highest mountains in eastern North America (Beamer and Lamb, 2020; Pyron et al., 2020, 2022; Pyron and Beamer, 2022a,b). They are morphologically distinguished from other plethodontids by unique skeleto-muscular specializations for feeding and burrowing (Schwenk and Wake, 1993). The center of species richness and diversity of *Desmognathus* is the southern Appalachian Mountains (Bruce, 2011). It is the only genus in the family containing highly aquatic and fully terrestrial species. Of special interest is the correlation between body size and habitat utilization in these salamanders. Generally, the larger species are more aquatic and the smaller are more terrestrial; the majority are streamside species of intermediate size that can be characterized as semiaquatic or semiterrestrial (Bruce, 2011). Habitat utilization of a species/population of *Desmognathus* can be evaluated by parameterization of data on frequency distributions of individuals along a gradient from stream to forest (Petranka and Smith, 2005; Milanovich et al., 2015; Hocking et al., 2020; Gould and Peterman, 2021).

One of the species included in the present study was assigned to *Desmognathus quadramaculatus* until recently (Black-bellied Salamander). The taxon has been split into four species, and the name "*quadramaculatus*" has been invalidated (Pyron and Beamer, 2022a). The Black-bellied Salamander populations under study herein fall within the range of the new species *Desmognathus amphileucus*.

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An unresolved question is the adaptive significance of the correlation of body size and habitat utilization in *Desmognathus*. Numerous authors have addressed this question by examining the role of intraguild interactions in structuring desmognathan communities (Bruce, 2011: table 7). The most comprehensive of such studies was a 4-yr experiment at Coweeta Hydrologic Laboratory, at sites supporting four of the five species occurring there (Hairston, 1986). Hairston manipulated population numbers of two species and examined the effects on the numbers of the other species. He concluded that the *Desmognathus* community was structured by intraguild interactions, mainly predation of larger on smaller species, but with a minor contribution of competition. Hairston suggested that the displacement of smaller by larger species from aquatic to terrestrial habitats on ecological time scales by intraguild interactions could represent the selective factor that has driven the adaptive radiation of *Desmognathus* on evolutionary time scales. However, this hypothesis was based on an evolutionary model that has undergone revision in a series of molecular analyses of plethodontid phylogenetics (e.g., Vieites et al., 2011; Wake, 2017). The phylogenetics of *Desmognathus* itself remains complex and unclear (Pyron et al., 2020, 2022). Thus, I reframe the question independently of phylogenetics, in terms of factors that contribute to the observed variation in body size and correlated phenotypic traits among species that subdivide the resources of the stream-to-forest habitat gradient.

The correlation between body size and habitat utilization in *Desmognathus* suggests that body size is the principal target of selection in a given focal habitat and evolves in conjunction with morphological, physiological, and behavioral traits that fine-tune adaptation to the habitat in question. Age at first reproduction and generation time may be the keys to understanding variation in body size and life history in *Desmognathus*. An evolutionary pathway to optimal body size is selection for an optimal age at first reproduction inasmuch as individual growth is curtailed at sexual maturation in desmognathans and other plethodontids (e.g., Tilley, 1980; Marvin, 2001; Staub, 2016).

Desmognathus salamanders exhibit sexual size dimorphism, wherein males attain sexual maturity at younger ages and smaller sizes than females, but in most species grow to larger sizes than females (Danstedt, 1975; Juterbock, 1978; Jones, 1986; Bruce, 2011). However, in the miniaturized species, *Desmognathus aeneus*, *Desmognathus organi*, and *Desmognathus wrighti*, adult males and females attain nearly equivalent maximum sizes (Hining and Bruce, 2005; Crespi et al., 2010). The current study is based mainly on the life-history traits of females, inasmuch as the source studies cited below are centered on body size, age, and demographics of female desmognathans.

The analyses described herein were designed to examine the roles of age at first reproduction and generation time in the adaptive radiation of *Desmognathus*. The goal was to test the hypothesis that variation in these traits effectively defines the extent of life-history variation in the genus through their trade-off relationships with growth and body size, productivity, and mortality rate. The evaluation of the relevant life-history variables has been carried out in the framework of the equal fitness paradigm (EFP), which is based on the premise that populations in ecological communities are equally fit and co-occur in steady states (Brown et al., 2018; Burger et al., 2021). As expressed in the latter two reports, the EFP is modeled on Kleiber's (1961) observation that metabolic rates in animals scale with body mass (M) according to $M^{0.75}$, approximately,

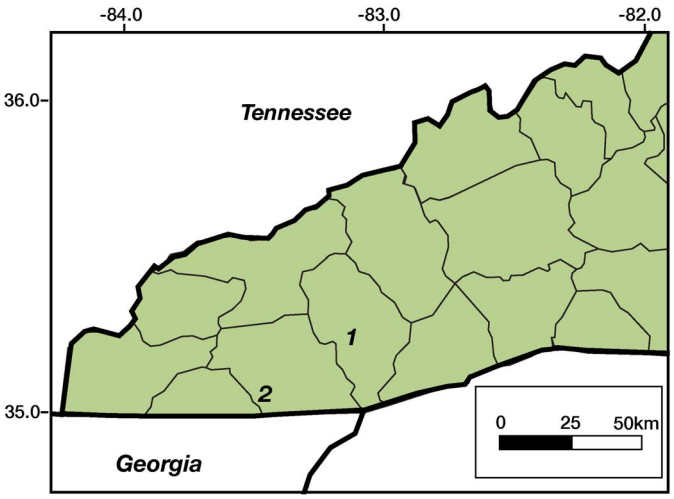

FIG. 1. The study areas in southwestern North Carolina. (1) Wolf Creek, Cowee Mountains, Jackson County. (2) Coweeta Creek and upper Nantahala River, Nantahala Mountains, Macon and Clay Counties. Coordinates are given in degrees north latitude and degrees west longitude (WGS 84).

such that the specific metabolic rate, that is, metabolic rate per unit of body mass, scales according to $M^{0.75}/M = M^{-0.25}$. Given that time is the reciprocal of rate, metabolic time scales to $M^{0.25}$ (Kleiber, 1961; Calder, 1984; Schmidt-Nielsen, 1984). Generation times and productivities in Brown et al. (2018) were calculated as reciprocals of mortality rates reported for a large data set of plant and animal mortality rates (McCoy and Gillooly, 2008). These provided a source for evaluating mortality rates in *Desmognathus* within the construct of the EFP.

MATERIALS AND METHODS

Study Populations.—The principal data sources for the study were published demographic evaluations of five species of *Desmognathus* that co-occur in the southern Blue Ridge Mountains of southwestern North Carolina (Hining and Bruce, 2005; Bruce, 2009, 2013, 2017, 2018, 2021, 2022). Assemblages of desmognathans were investigated at two sites: 1) Wolf Creek on Cullowhee Mountain, a spur of the Cowee Mountains in Jackson County; and 2) Coweeta Creek and adjacent sections of the upper Nantahala River basin in the southern Nantahala Mountains in Macon and Clay Counties (Fig. 1). I refer to these as the Wolf Creek and Coweeta assemblages (Figs. 2, 3). Exact locality data and descriptions of the sites are provided in the cited papers. The Wolf Creek assemblage included *D. amphileucus*, *Desmognathus monticola*, and *Desmognathus ocoee*. These three species occurred also at Coweeta together with *D. aeneus* and *D. wrighti*. In addition, *Desmognathus marmoratus* is found in the Nantahala watershed, but not at Coweeta Creek, and was not included in the cited studies because of incomplete life history data.

Given the premise of the EFP that populations are in a steady state, the populations of the species of *Desmognathus* under consideration in the Cowee and Nantahala Mountains were assumed to be relatively stationary during the period of study (Bruce, 2013, 2021). This has been best documented in population counts of four species of *Desmognathus* in the Nantahalas at Coweeta Hydrologic Laboratory conducted over 23–27 yr (Hairston and Wiley, 1993; Hairston, 1996; Dixon and Pechmann, 2005). Fortuitously, these surveys were conducted

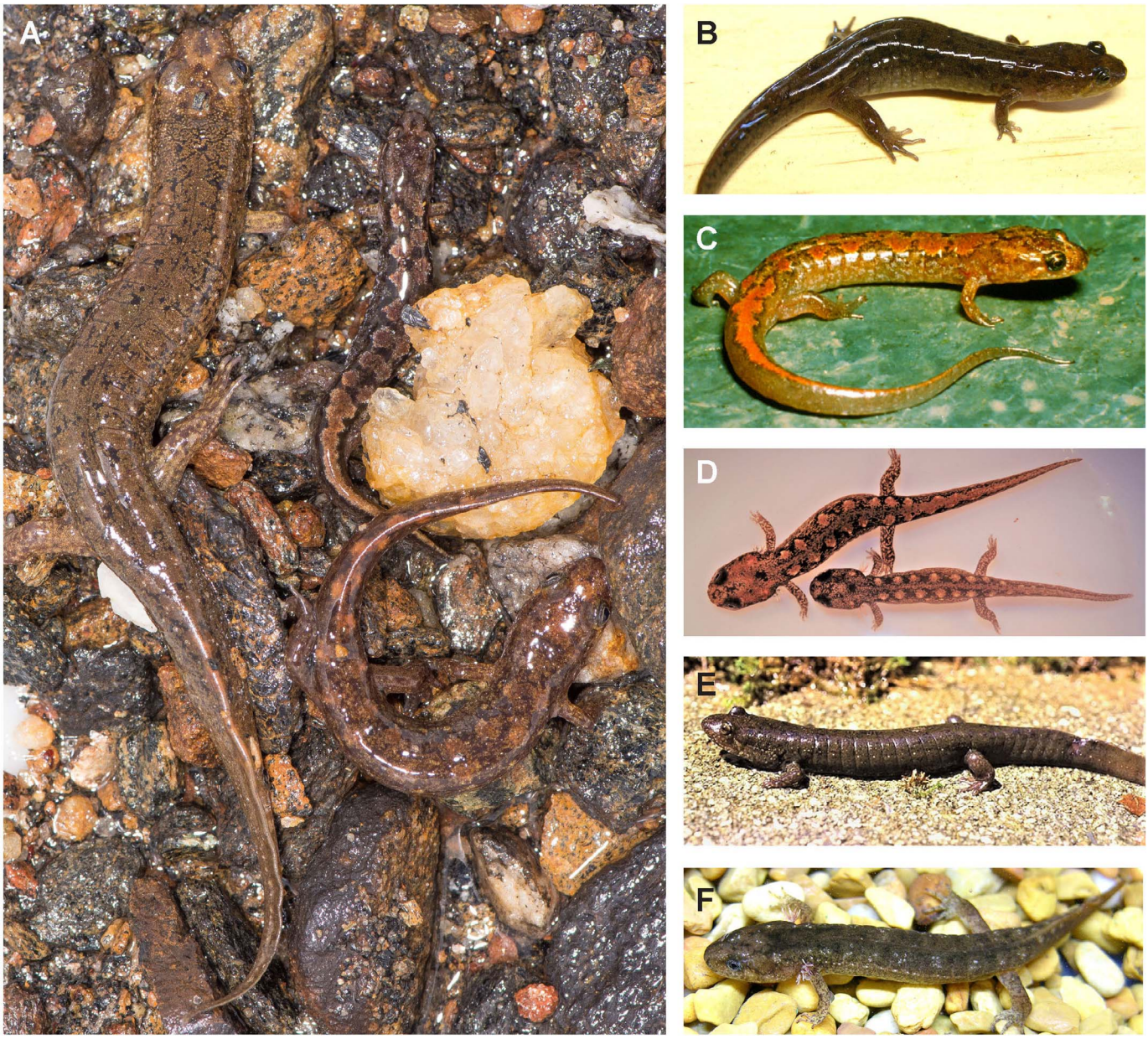

FIG. 2. Representative *Desmognathus* from Wolf Creek and Coweeta/Nantahala. Body sizes, when given, are estimates based on field measurements. (A) The three species of Wolf Creek *Desmognathus* photographed against the substrate of a tributary stream. Subadults of *D. amphileucus* (left) and *D. monticola* (below right); adult of *D. ocoee* (above right). (B–F) Coweeta-Nantahala *Desmognathus*. (B) Adult *D. monticola*. (C) Adult *D. ocoee*. (D) First-year larvae of *D. monticola* (15 mm SL) (above) and *D. ocoee* (12 mm SL). (E) Adult *D. amphileucus*. (F) Third-year larva of *D. amphileucus* (32 mm SL).

during the years when my field work was carried out at Coweeta.

Application of the Equal Fitness Paradigm.—The variables evaluated in the source publications included age in years (x) and age at first reproduction (x^*), which were estimated directly from salamander specimens by skeletochronology and dissection of reproductive organs. Body-size measurements taken on living salamanders included standard length (SL), measured to the nearest 0.1 mm from the tip of the snout to the posterior edge of the cloacal slit, and mass, recorded as "wet weight" (W) to the nearest 0.001 g. Variables estimated from the demographic analyses included survival (l_x column of life table), fecundity (m_x column of life table), net reproductive rate (R_0, equaling the sum of the $l_x m_x$ column of the life table), and generation time (G, equaling the sum of the $xl_x m_x$ column of the life table divided by R_0).

For three of the species—*D. monticola*, *D. ocoee*, and *D. amphileucus*—female growth was evaluated by Gompertz growth equations fitted to the skeletochronological data; that is, $SL_x = SL_0 \cdot \exp((\beta/\alpha) \cdot (1-\exp(-\alpha \cdot x)))$ (Bruce, 2017, 2021, 2022). For *D. aeneus* and *D. wrighti* female growth was evaluated according to frequency distributions of body size (Hining and Bruce, 2005; Bruce, 2009).

The basic equation of the EFP, from Brown et al. (2018), is

$$E = GBQF,$$

where E = energetic fitness, defined as the transfer of energy in kJ/g per generation to surviving offspring, G = generation time

FIG. 3. (A) Tributary of the upper Nantahala River. Six species of *Desmognathus* and four other species of plethodontid salamanders co-occur within the field of view of this photograph. (B) Adults of the miniaturized Coweeta/Nantahala species, *D. wrighti* (left) and *D. aeneus* (each about 25 mm SL). (C) Terrestrial egg clutch of *D. aeneus* attended by the female parent.

(yr), B = rate of biomass production in g g^{-1} yr^{-1}, Q = energy density of biomass in kJ/g, and F = fraction of biomass produced that ends up in surviving offspring in the next generation. Thus, if $E/Q = 1$ = fitness in grams/gram/generation under the EFP, then F is defined as

$$F = 1/GB.$$

For a large variety of organisms, scaling functions, based on log–log least-squares regressions, were

$$G = 3.0M^{0.25} \text{ and } B = 2.54M^{-0.25}$$

(Brown et al., 2018). I refer to these as EFP functions. Solving for F yields

$$F = 1/GB = 1/(3.0M^{0.25})(2.54M^{-0.25}) = 0.13.$$

In the source studies on *Desmognathus*, in which body length was recorded as standard length (SL), I transformed SL to wet body mass (W) by least-squares regression of ln W on ln SL; that is, $\ln(W) = \ln(a) + b \cdot \ln(\text{SL})$, as reported for four of the five species (Bruce, 2018: table 1). The data for the fifth, *D. wrighti*, was taken from my archived, unpublished field notes (see Acknowledgments). The tight fits of the regressions ($R^2 \geq 0.98$ for each species/population) lent confidence to the accuracy of the mass estimates. Inasmuch as mass was recorded as wet weight (W), I estimated dry weight (M) by multiplying each wet weight by 0.3125 (i.e., $M = W/3.2$), given that the energy density of biomass ≈22.4 kJ/g dry weight ≈ 7 kJ/g wet weight (Burger et al., 2021). However, Brown et al. (2018) used $M = 0.25W$, which, if substituted for $M = 0.3125W$, has only a minor effect on the equations for G and B. In evaluating generation time and productivity, I performed least-squares regressions of $\log_{(10)}(G)$ and $\log_{(10)}(B)$ on $\log_{(10)}(M)$. Although values of G were taken directly from the demographic analyses (Bruce, 2013, 2017, 2021, 2022), estimates of B were based on the equation $B = 1/GF$, wherein the consensus value of F is approximately 0.13 in the EFP model (Brown et al., 2018). The latter authors reported that F is constrained between 0.1 and 0.5. Thus I conducted regressions of B on dry body mass for values of $F = 0.1$, 0.13, and 0.5.

Given that ages at first reproduction were estimated directly by skeletochronology and dissection, I bypassed uncertainties in some parameters of the EFP model by conducting least-squares regressions of age at first reproduction (x^*) on dry body mass. I

TABLE 1. Elements of the EFP regressions of generation time (G) and productivity (B) on body mass (M) for five species of *Desmognathus*. The values of wet mass (W_x), dry mass (M_x), and productivity (B_x) were calculated for ages (x) equal to generation time. Values of B_x were calculated for F values of 0.1, 0.13, and 0.5, representing the fraction of lifetime biomass production transferred to surviving offspring in the next generation. The values of G, x, and W_x were taken from Bruce (2013, 2017, 2018, 2021, 2022).

Species population	G (yr)	x (yr)	SL_x (mm)	W_x (g)	M_x (g)	$B_{x(0.1)}$ (g g^{-1} yr^{-1})	$B_{x(0.13)}$ (g g^{-1} yr^{-1})	$B_{x(0.5)}$ (g g^{-1} yr^{-1})
D. amphileucus								
Wolf Creek	8.6	8.6	77.13	9.85	3.08	1.163	0.894	0.232
Coweeta	10.2	10.2	85.00	13.09	4.09	0.980	0.754	0.196
D. monticola								
Wolf Creek	7.46	7.46	63.97	5.09	1.59	1.340	1.031	0.268
Coweeta	8.17	8.17	69.28	6.27	1.95	1.224	0.941	0.245
D. ocoee								
Wolf Creek	4.84	4.84	39.74	0.930	0.291	2.066	1.589	0.413
Coweeta	4.80	4.80	41.86	1.137	0.355	2.083	1.603	0.417
D. aeneus, Coweeta	4.33	4.33	26.00	0.300	0.094	2.309	1.776	0.462
D. wrighti, Coweeta	4.02	4.02	25.40	0.256	0.080	2.490	1.915	0.498

then derived values of B for $F = 0.13$ only, that is, $B = 1/(x^* \cdot 0.13)$. In order to test the efficacy of size at initial reproduction as a predictor of adult body size, I generated statistics on body sizes of adult females of *D. amphileucus*, *D. monticola*, and *D. ocoee* from the source skeletochronological databases. For *D. aeneus* and *D. wrighti* I estimated the comparable statistics from the frequency distributions of standard lengths.

From the demographics in the source data sets, I estimated scaling functions ($Z = aM^b$) of mortality rate (Z) on dry body mass (M) of adult females of *Desmognathus* at ages equal to generation time. These were determined for annual reproductive schedules in *D. ocoee*, *D. aeneus*, and *D. wrighti*, and for biennial schedules in *D. monticola* and *D. amphileucus*. For consistency with the other species, I adjusted survival schedules of *D. ocoee* and *D. monticola* to constant instantaneous mortality rates (wherein $R_0 = 1.0$), which averages out the age-specific differential mortality rates incorporated into the published life tables of these two species (Bruce, 2017, 2021). I then compared the least-squares regression of $\log_e$ mortality rate on $\log_e$ dry body mass of *Desmognathus* with that for "fish" reported in McCoy and Gillooly (2008), given that the latter authors provided no data on amphibians. For consistency with the procedures of McCoy and Gillooly, in this analysis only I transformed the empirical values of wet body mass to dry body mass according to $M_x = 0.25W_x$.

In evaluating G, B, and x^* I followed Brown et al. (2018) in converting variables to common logarithms, whereas in evaluating Z I followed McCoy and Gillooly (2008) in converting variables to natural logarithms. All statistical analyses were carried out with SYSTAT 13.2 (SYSTAT Software, Inc.).

RESULTS

The values of the empirical and derived variables entered into the analyses of G and B are provided in Table 1, and those of the analyses of x^* and B are given in Table 2. The scaling functions of G, B, and x^* with body mass (M) are listed in Table 3. It is noteworthy that adult females of the smallest and largest species of *Desmognathus* in the Cowee and Nantahala Mountain assemblages varied in body mass by factors $\geq$35 and in age at first reproduction by a factor of 3. For survival to age at first reproduction, the decrease from the two smallest species ($l_{x^*} \approx 0.1$) that reproduce at age 3 yr to the largest ($l_{x^*} \approx 0.03$) that reproduce at ages 7–8 and 8–10 yr was indicative of a relatively high rate of annual survival in the genus generally.

In evaluating G and B of *Desmognathus*, I compared the least-squares regression lines of the log-transformed values of the variables to those of the large samples of organisms included in the EFP regressions (Brown et al., 2018; Fig. 4). For *Desmognathus,* the regressions of $\log G$ and $\log B$ on $\log M$ yielded regression coefficients (b) of $+0.227$ and -0.227, respectively (Table 3); the regression lines bordered the upper and lower margins of the scatter of values around the EFP regression lines (Brown et al., 2018: Figs. 2, 3). For the smallest species, *D. aeneus* and *D. wrighti,* the EFP G values were 1.66 and 1.60 yr versus the empirical estimates of 4.33 and 4.02 yr, respectively. For the large *D. amphileucus* the G values of the Wolf Creek and

TABLE 2. Elements of the EFP regressions of age at first reproduction (x^*) and productivity (B) on body mass (M) for five species of *Desmognathus*. Values of B_{x^*} were calculated for $F = 0.13$ only. The values of x^*, SL_{x^*}, and l_{x^*} were taken from Bruce (2013, 2017, 2018, 2021, 2022). The discrepancy in the l_{x^*} estimates of *D. ocoee* is a result of alternative methods of constructing life tables for this species (Bruce 2013, 2017). Values of x^* have been rounded to the nearest whole number from mean values estimated for Wolf Creek *D. monticola* and *D. amphileucus* (Bruce, 2021, 2022)

Species population	x^* (yr)	SL_{x^*} (mm)	l_{x^*}	W_{x^*} (g)	M_{x^*} (g)	B_{x^*} (g g^{-1} yr^{-1})
D. amphileucus						
Wolf Creek	8	74.6	0.018	8.912	2.785	0.961
Coweeta	9	81.1	0.020	11.40	3.562	0.855
D. monticola						
Wolf Creek	6	58.5	0.032	3.932	1.229	1.282
Coweeta	6	61.2	0.031	4.366	1.364	1.282
D. ocoee						
Wolf Creek	4	35.4	0.024/0.06	0.780	0.244	1.923
Coweeta	4	38.6	0.024/0.06	0.947	0.296	1.923
D. aeneus, Coweeta	3	23.0	0.094	0.210	0.0656	2.564
D. wrighti, Coweeta	3	21.0	0.114	0.161	0.0503	2.564

TABLE 3. Scaling functions and least-squares regressions of generation time (G), age at first reproduction (x^*), productivity (B), and mortality rate (Z) on dry body mass (M) for Wolf Creek and Coweeta *Desmognathus*.

		Least-squares regressions of the scaling functions				
Scaling function	F	ANOVA:	R^2	F ratio	df	P
$G = 6.839M^{0.227}$	–	$\log_{10} G = 0.835 + 0.227 \log_{10} M$	0.962	151.7	1, 6	<0.001
$B_F = 1.125M^{-0.227}$	0.13	$\log_{10} B_{0.13} = 0.051 - 0.227 \log_{10} M$				
$B_F = 1.462M^{-0.227}$	0.10	$\log_{10} B_{0.10} = 0.165 - 0.227 \log_{10} M$				
$B_F = 0.292M^{-0.227}$	0.50	$\log_{10} B_{0.50} = -0.534 - 0.227 \log_{10} M$				
$x^* = 5.929M^{0.255}$	–	$\log_{10} x^* = 0.773 + 0.255 \log_{10} M$	0.975	235.4	1, 6	<0.001
$B_F = 1.297M^{-0.255}$	0.13	$\log_{10} B_{0.13} = 0.113 - 0.255 \log_{10} M$				
$Z = 0.545M^{-0.134}$		$\ln Z = -0.607 - 0.134 \ln M$	0.935	86.7	1, 6	<0.001

Coweeta populations were 4.08 and 4.37 yr (EFP) versus 8.6 and 10.2 yr (empirical). Similar differences applied to the intermediate-sized species, *D. monticola* (3.18, 3.31 vs. 7.46, 8.17 yr) and *D. ocoee* (2.20, 2.32 vs. 4.84, 4.8 yr). The differences illustrate 1) the lengthy generation times relative to body size over the entire size range of the genus *Desmognathus*, at least in these assemblages, and 2) the corresponding lower metabolic rates and productivities of these salamanders. The differences held across the range of F values evaluated in the regression analyses, although the upper limit ($F = 0.5$) is probably not realized in vertebrate animals.

Substitution of x^* for G in the regression analyses (Fig. 5) generated equations with tighter fits of the data to the regression line (Table 3). The exponents of the scaling functions (±0.255) were essentially identical to those predicted (±0.25) by the EFP.

The regression line of desmognathan mortality fell below that of the fish regression line (Fig. 6) and bordered the lower edge of the point scatter of the fish regression (McCoy and Gillooly, 2008: Fig. 2b). The slope of the *Desmognathus* regression was less than that of fish, −0.134 vs. −0.27. The latter was close to the predicted value of −0.25.

In the three species in which age was determined by skeletochronology (*D. ocoee*, *D. monticola*, *D. amphileucus*), the mean standard lengths of adult females varied from 0.99 to 1.08 times the value of SL_{x^*}. In the remaining two species, *D. aeneus* and *D. wrighti*, in which estimates of age/size at first reproduction were less precisely estimated from body-size

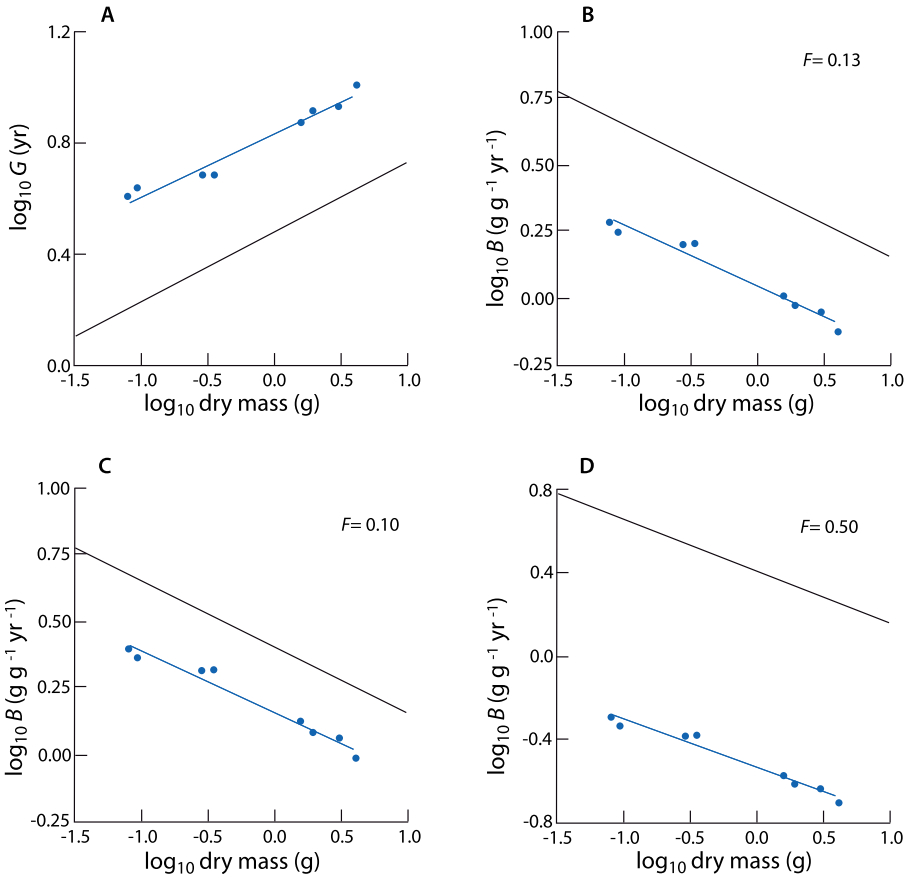

FIG. 4. Blue regression lines and symbols: ordinary least-squares regressions of $\log_{10}$ transforms of the scaling functions of generation time (G) and productivity (B) on dry body mass (M), from Table 1. Black regression lines represent the $\log_{10}$ transforms of the consensus scaling functions $G = 3.0M^{0.25}$ and $B = 2.54M^{-0.25}$ from Brown et al. (2018). (A) G = generation time. (B, C, D) B = productivities for several values of F, where F = fraction of productivities allocated to surviving offspring.

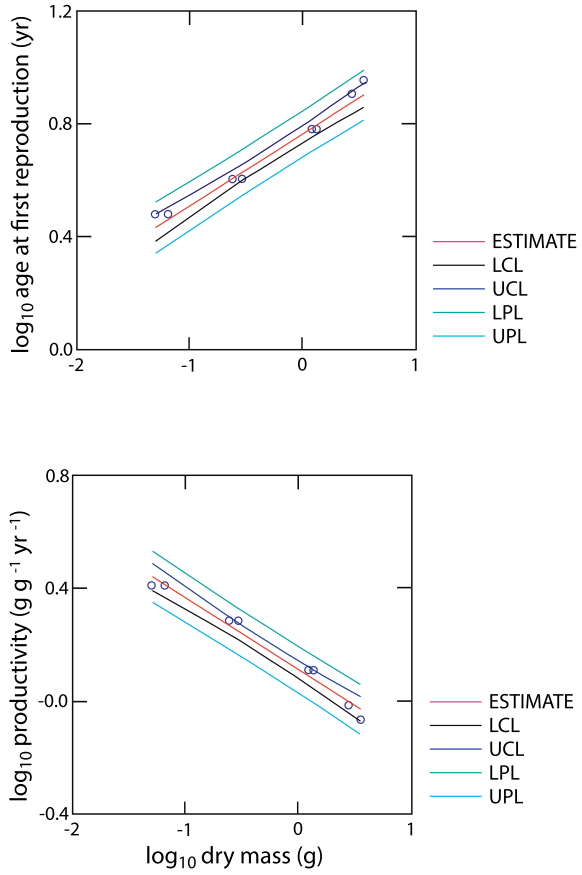

FIG. 5. Ordinary least-squares regressions of $\log_{10}$ transforms of the scaling functions of age at first reproduction (x^*) and productivity (B) on dry body mass (M), from Table 2. LCL, UCL: lower, upper confidence limits. LPL, UPL: lower, upper prediction limits.

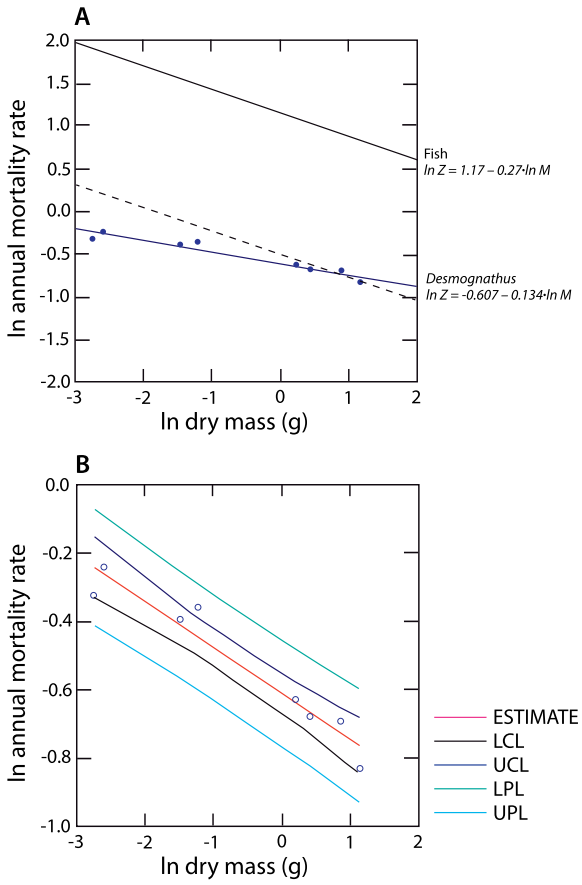

FIG. 6. (A) Solid black line: least-square consensus regression of $\log_e$ mortality rate (ln Z) on $\log_e$ body mass of the fish data set of McCoy and Gillooly (2008). Dashed black line: approximate lower limit of the point scatter of the fish data. See Fig. 2b in McCoy and Gillooly (2008). Blue line and symbols: least-squares regression of $\log_e$ mortality rate on $\log_e$ body mass of Wolf Creek and Coweeta *Desmognathus*, from life tables. Z values for *Desmognathus* calculated as mortality rate over average life span; that is, age = generation time (G). (B) Details of the *Desmognathus* regression. LCL, UCL: lower, upper confidence limits. LPL, UPL: lower, upper prediction limits.

distributions, the factors were 1.10 and 1.13, respectively (Table 4). The ratios of M_{mean}/M_{x^*} were more variable (1.04 to 1.41), as expected for units of mass where $M \approx a \cdot \text{SL}^3$. Given the wide use of standard length as a metric of body size in salamanders, this index of size at first reproduction demonstrated the strong effect of age/size at first reproduction in curtailing growth and setting limits to adult body size in females of *Desmognathus*.

TABLE 4. Adult female body sizes of the five species of *Desmognathus*. For *D. amphileucus*, *D. monticola*, and *D. ocoee* the data on standard lengths (SL) were from skeletochronological data sets in the source publications. For *D. aeneus* and *D. wrighti* the comparable data were based on size-frequency data in Hining and Bruce (2005) and Bruce (2009). Dry body masses ($M = 0.3125W$) were estimated from regressions of wet weight (W) on SL (Bruce, 2018).

				SL (mm)			M (g)		
Species population	SL_{x^*} (mm)	M_{x^*} (g)	n	Range	Mean	SD	Range	Mean	SD
D. amphileucus									
Wolf Creek	74.6	2.785	28	70.8–85.1	78.5	4.473	2.382–4.131	3.276	0.550
Coweeta	81.1	3.562	9	77.7–94.6	87.2	5.201	3.141–5.608	4.448	0.765
D. monticola									
Wolf Creek	58.5	1.229	27	48.7–65.0	58.0	3.923	0.722–1.667	1.214	0.224
Coweeta	61.2	1.364	17	59.1–70.2	63.9	3.239	1.232–2.035	1.557	0.230
D. ocoee									
Wolf Creek	35.4	0.244	19	28.7–41.4	35.6	3.678	0.136–0.376	0.253	0.071
Coweeta	38.6	0.296	17	33.8–46.2	39.6	3.840	0.202–0.498	0.325	0.089
D. aeneus, Coweeta	23.0	0.0656	24	23.0–28.0	25.4	1.345	0.066–0.116	0.088	0.014
D. wrighti, Coweeta	21.0	0.0503	22	21.0–25.0	23.7	1.241	0.046–0.076	0.066	0.010

Discussion

Within the framework of the EFP the desmognathan salamanders under consideration exhibit greater ages at first reproduction, lengthier generation times, lower growth/productivity rates, and lower mortality rates than similar-sized vertebrates. These traits place *Desmognathus* at the slow end of the fast–slow axis of life-history variation (Healy et al., 2019; Wright et al., 2020). This is to be expected for plethodontid salamanders constrained by lunglessness and low metabolic rates (Feder, 1983; Gatten et al., 1992; Gifford, 2016). Generation time is determined by age at first reproduction in concert with schedules of growth, reproduction, and survival at subsequent ages. Animal generation times are usually less than 1.5 times age at first reproduction (Stearns, 1992). This was the case for all five species of *Desmognathus* in the present study.

Female growth in *Desmognathus*, as in other plethodontids, slows markedly at sexual maturation; thus age and size at first reproduction serve as a control of adult body size. In some fishes, and probably some amphibians, age at first reproduction may be an outcome of the synergistic action of trade-offs between 1) growth and reproductive allocation and 2) survival and reproductive allocation (Roff et al., 2006). Under the EFP these reduce to a trade-off between generation time ($\approx$1/mortality rate) and productivity (growth, reproduction), as defined by McCoy and Gillooly (2008) and Brown et al. (2018). In earlier papers I examined potential trade-offs among these traits in the species of *Desmognathus* included herein (Bruce, 2013, 2018). In the latter report I concluded that larger body sizes in the more aquatic species are attained by delay in sexual maturation, allowing for continued growth and higher survival. The larger species provide greater provisioning of offspring at a cost of relatively lower fecundity, which may be compensated by higher offspring survival. Although growth of smaller species is truncated by earlier maturation, they gain a head start in reproduction, by as much as 5–7 yr in *D. aeneus*/*D. wrighti* versus *D. amphileucus*.

A significant feature of life histories in *Desmognathus* are correlations between 1) body size and age at first reproduction and 2) body size and habitat utilization. The species of *Desmognathus* sort by body size into stream, streamside, and forest species (Bruce, 2011: Table 1; Weaver et al., 2020: Table 2). Stream species spend 2–4 yr as aquatic larvae and tend to grow to larger adult sizes than other desmognathans. The largest stream species is *D. amphileucus,* exemplified by the Coweeta populations; however, there are populations of other species of Black-bellied Salamanders that are smaller in body size, younger in age at first reproduction, but equally aquatic (Camp et al., 2000; Beachy and Bruce, 2003; Camp and Marshall, 2006; Pyron and Beamer, 2022a). Another stream form is the even more aquatic *D. marmoratus*, which tends to be somewhat smaller than *D. amphileucus* (Martof, 1962). A fourth stream species, *Desmognathus welteri*, is a large salamander that approaches *D. amphileucus* in adult size (Redmond, 1980; Juterbock, 1984). All of the stream species are essentially restricted to the southern Appalachian Mountains. Large body size, lunglessness, and skeleto-muscular specializations in these species are traits that facilitate bottom crawling and head wedging beneath rocks in high-gradient mountain streams.

There are three forest-dwelling terrestrial species of *Desmognathus* that represent the smallest members of the genus and rank among the smallest of the world's salamanders. They occur mainly in the southern Appalachians, with *D. aeneus* extending southwestward into central Alabama. In both *D. aeneus* and *D. wrighti,* as noted herein, females reproduce initially at age 3 at live weights of only 0.25–0.33 g (Hining and Bruce, 2005; Bruce, 2009). Body sizes and life history of the third species, *D. organi*, are similar to those of *D. wrighti* (Crespi et al., 2010). Small body size in these species is likely an adaptation to life on the forest floor in humid mountain forests, where the salamanders co-occur with other, larger, terrestrial plethodontids, especially *Plethodon*. Small size may represent an outcome of competition with the larger species, which provides these tiny desmognathans with a resource base (e.g., food, cover objects, nesting sites) unexploited by the larger forms (Hairston, 1981; Rossell et al., 2018).

Streamside species of intermediate body size account for 20 of the 30 named species (and many candidate species) of *Desmognathus,* and occur throughout the range of the genus in eastern North America. They have abbreviated larval periods $\leq$1.0 yr. Sexual maturation in many streamside species is apparently attained at 3–4 yr, but most estimates are based on frequency distributions of body sizes that may be imprecise (see accounts in Lannoo, 2005). However, for two populations of *D. ocoee* located near those at Wolf Creek and Coweeta, Tilley (1980), using long-term mark–recapture to produce life tables, estimated ages at first reproduction of 4 and 5 yr, and generation times of 5.6 and 7.5 yr, respectively. Female body sizes, M, at $x = G$ were 0.154 and 0.246 g, approximately, based on growth curves in Tilley (1980). Application of the EFP scaling function to these data yields estimates of generation times of only 1.9 and 2.1 yr, slightly lower than my estimates for the Wolf Creek and Coweeta populations.

One of the larger and more aquatic streamside species is *D. monticola*, wherein age at first reproduction is 5–7 yr in females (Bruce, 2021). Adult female body sizes are similar to those of the stream species *Desmognathus folkertsi* and *D. marmoratus*. The largest streamside species, *Desmognathus brimleyorum,* attains sizes similar to *D. amphileucus*, but apparently has life-history traits like those of other streamside forms (Means, 1974). Thus, there is considerable overlap in adult body size between stream and streamside species, as documented in the cited papers, although the former generally grow to larger sizes. However, there is essentially no overlap in adult size of streamside and the three forest species, especially females (Bruce, 2009; Crespi et al., 2010).

The wider range of habitat utilization of streamside species vis-à-vis their stream and forest counterparts is documented in studies of frequencies of individuals found along horizontal transects extending from streams into adjacent forests (Hairston, 1949: Tables 4, 5; Hairston, 1980: Table 5; Petranka and Smith, 2005: Fig. 3). Hairston (1980) showed that two such species ranged further from stream into forest during rainy weather. Such observations suggest that dispersal pathways available to streamside forms include the streams of origin as well as forest corridors extending outward from these streams. The intermediate body sizes in conjunction with the abbreviated larval phases may represent adaptations that facilitate dispersal and account for the wide distributions of these species (Bruce, 2011). This hypothesis has been examined recently under the heading of climatic niche evolution (Weaver et al., 2020). The latter authors contended that short larval periods in streamside species promote adaptation to drier climatic niches beyond the southern Appalachian Mountains. Alternatively, the retention of a brief larval phase in the life cycles of streamside species may represent a strategy for survival through the first winter.

Reportedly, among the Nantahala species the streamside forms *D. ocoee* and *D. monticola* have stronger responses (abundance, occupancy) to such broad-scale variables as elevation, slope, aspect, and stream order, whereas the aquatic *D. amphileucus* has stronger responses to fine-scale, water-quality variables, including pH, conductivity, and temperature (Gould and Peterman, 2021). The authors contended that species of *Desmognathus* with short larval periods and more terrestrial adult phases respond more strongly to broad-scale versus fine-scale variables, but they did not relate the difference to dispersal ability.

Over the size range of the five species in the current data set, the lengthier generation times, lower productivities, and lower mortalities than predicted by the EFP reflect trade-offs among survival, growth, and reproductive rates in these salamanders. Although fecundity (m_x values of the life table) is not directly represented in the output of the EFP, such data are available for the Wolf Creek and Coweeta desmognathans (Bruce, 2018). Within the construct of the EFP, metabolic life histories that include trends in survival, body mass, and fecundity have been developed graphically for a diversity of animals, but not amphibians (Burger et al., 2021: Fig. 4). I have generated such metabolic life histories for *D. amphileucus* (Bruce, 2022), and am continuing to fill in gaps of metabolic life-history data for other desmognathan species in the Wolf Creek and Coweeta assemblages.

The species/populations of the present study include a small fraction only of desmognathan diversity, but encompass the full range of body sizes represented in the genus. Given the strong association of body size and habitat utilization in *Desmognathus*, I have suggested that body size has been the principal target of selection in the adaptive radiation of the genus (Bruce, 2009). Age at first reproduction is a key variable in the generation of interspecific differentiation in body size in these salamanders, as demonstrated herein by the tight relationship in females between body size at first reproduction and mean adult body size. However, for many species (and candidate species) of *Desmognathus* the life histories and demographics are imperfectly known, especially age-indexed reproductive and survival schedules. Such data would be helpful not only in expanding our knowledge of the evolutionary ecology of this unique salamander genus, but in identifying factors critical to the conservation biology of its component species, which now is a high priority.

NOTE ADDED IN PROOF. *Desmognathus ocoee* has recently been split into several species (Pyron and Beamer, 2022b). The Coweeta population is retained in *D. ocoee*, but the Wolf Creek population has been assigned to *D. perlapsus*.

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Literature Cited

AmphibiaWeb. 2022. https://amphibiaweb.org. University of California, Berkeley.

Beachy, C. K., and R. C. Bruce. 2003. Life history of a small form of the plethodontid salamander *Desmognathus quadramaculatus*. Amphibia-Reptilia 24:13–26.

Beachy, C. K., T. J. Ryan, and R. M. Bonett. 2017. How metamorphosis is different in plethodontids: larval life history perspectives on life-cycle evolution. Herpetologica 73:252–278.

Beamer, D. A., and T. Lamb. 2020. Towards rectifying limitations on species delineation in dusky salamanders (*Desmognathus*: Plethodontidae): an ecoregion-drainage sampling grid reveals additional cryptic clades. Zootaxa 4734(1):1–61.

Brown, J. H., C. A. S. Hall, and R. M. Sibly. 2018. Equal fitness paradigm explained by a trade-off between generation time and energy production rate. Nature Ecology & Evolution 2:262–268.

Bruce, R. C. 2009. Life-history contributions to miniaturization in the salamander genus *Desmognathus* (Urodela: Plethodontidae). Copeia 2009:714–723.

———. 2011. Community assembly in the salamander genus *Desmognathus*. Herpetological Monographs 25:1–24.

———. 2013. Size-mediated tradeoffs in life-history traits in dusky salamanders. Copeia 2013:262–267.

———. 2017. A provisional model of demography in *Desmognathus ocoee* (Amphibia, Plethodontidae). Copeia 105:634–639.

———. 2018. Interspecific variation in reproductive effort in two assemblages of dusky salamanders. Journal of Herpetology 52:209–214.

———. 2021. Alternative demographic models for two populations of the Seal Salamander, *Desmognathus monticola*. Ichthyology & Herpetology 109:84–91.

———. 2022. A female-centered evaluation of growth, survival, reproduction, and demography in the salamander *Desmognathus quadramaculatus*. Ichthyology & Herpetology 110:439–448.

Burger, J. R., C. Hou, C. A. S. Hall, and J. H. Brown. 2021. Universal rules of life: metabolic rates, biological times and the equal fitness paradigm. Ecology Letters 24:1262–1281.

Calder, W. A. III. 1984. Size, Function, and Life History. Harvard University Press, USA.

Camp, C. D., and J. L. Marshall. 2006. Reproductive life history of *Desmognathus folkertsi* (Dwarf Black-bellied Salamander). Southeastern Naturalist 5:669–684.

Camp, C. D., J. L. Marshall, and R. M. Austin, Jr. 2000. The evolution of adult body size in black-bellied salamanders (*Desmognathus quadramaculatus* complex). Canadian Journal of Zoology 78:1712–1722.

Crespi, E. J., R. A. Browne, and L. J. Rissler. 2010. Taxonomic revision of *Desmognathus wrighti* (*Caudata*: *Plethodontidae*). Herpetologica 66:283–295.

Dani, K. G. S., and U. Kodandaramaiah. 2017. Plant and animal reproductive strategies: lessons from offspring size and number tradeoffs. Frontiers in Ecology and Evolution 5:38. doi:10.3389/fevo.2017.00038.

Danstedt, R. T., Jr. 1975. Local geographic variation in demographic parameters and body size of *Desmognathus fuscus* (Amphibia: Plethodontidae). Ecology 56:1054–1067.

Dixon, P. M., and J. H. K. Pechmann. 2005. A statistical test to show negligible trend. Ecology 86:1751–1756.

Feder, M. E. 1983. Integrating the ecology and physiology of plethodontid salamanders. Herpetologica 39:291–310.

Gatten, R. E., Jr., K. Miller, and R. J. Full. 1992. Energetics at rest and during locomotion. Pp. 314–377 in M. E. Feder and W. W. Burggren (eds.). Environmental Physiology of the Amphibia. University of Chicago Press, USA.

Gifford, M. E. 2016. Physiology of plethodontid salamanders: a call for increased efforts. Copeia 104:42–51.

Gould, P. R., and W. E. Peterman. 2021. Life history mediates the effects of habitat variation on salamander abundance: a multiscale assessment. Landscape Ecology 36:749–761.

Hairston, N. G. 1949. The local distribution and ecology of the plethodontid salamanders of the southern Appalachians. Ecological Monographs 19:47–73.

———. 1980. Species packing in the salamander genus *Desmognathus*: What are the interspecific interactions involved? American Naturalist 115:354–366.

———. 1981. An experimental test of a guild: salamander competition. Ecology 62:65–72.

HAIRSTON, N. G., SR. 1986. Species packing in *Desmognathus* salamanders: experimental demonstration of predation and competition. American Naturalist 127:266–291.

———. 1996. Predation and competition in salamander communities. Pp. 161–189 in M. L. Cody and J. A. Smallwood (eds.), Long-Term Studies of Vertebrate Communities. Academic Press, USA.

HAIRSTON, N. G., SR., AND R. H. WILEY. 1993. No decline in salamander (Amphibia: Caudata) populations: a twenty-year study in the southern Appalachians. Brimleyana 18:59–64.

HEALY, K., T. H. G. EZARD, O. R. JONES, R. SALGUERO-GÓMEZ, AND Y. M. BUCKLEY. 2019. Animal life history is shaped by the pace of life and the distribution of age-specific mortality and reproduction. Nature Ecology & Evolution 3:1217–1224.

HINING, K. J., AND R. C. BRUCE. 2005. Population structure and life history attributes of syntopic populations of the salamanders *Desmognathus aeneus* and *Desmognathus wrighti* (Amphibia: Plethodontidae). Southeastern Naturalist 4:679–688.

HOCKING, D. J., J. A. CRAWFORD, W. E. PETERMAN, AND J. R. MILANOVICH. 2020. Abundance of montane salamanders over an elevational gradient. Ecology and Evolution 11:1–14. https://doi.org/10.1002/ece3.7142.

JONES, R. L. 1986. Reproductive biology of *Desmognathus fuscus* and *Desmognathus santeetlah* in the Unicoi Mountains. Herpetologica 42: 323–334.

JUTERBOCK, J. E. 1978. Sexual dimorphism and maturity characteristics of three species of *Desmognathus* (Amphibia, Urodela, Plethodontidae). Journal of Herpetology 12:217–230.

———. 1984. Evidence for the recognition of specific status for *Desmognathus welteri*. Journal of Herpetology 18:240–255.

KLEIBER, M. 1961. The Fire of Life: an Introduction to Animal Energetics. John Wiley & Sons, Inc., USA.

KOZAK, K. H. 2017. What drives variation in plethodontid salamander species richness over space and time? Herpetologica 73:220–228.

LANNOO, M. (ed.). 2005. Amphibian Declines: the Conservation Status of United States Species. University of California Press, USA.

MARTOF, B. S. 1962. Some aspects of the life history and ecology of the salamander *Leurognathus*. American Midland Naturalist 67:1–35.

MARVIN, G. A. 2001. Age, growth, and long-term site fidelity in the terrestrial plethodontid salamander *Plethodon kentucki*. Copeia 2001: 108–117.

MCCOY, M. W., AND J. F. GILLOOLY. 2008. Predicting natural mortality rates of plants and animals. Ecological Letters 11:710–716.

MEANS, D. B. 1974. The status of *Desmognathus brimleyorum* Stejneger and an analysis of the genus *Desmognathus* (Amphibia: Urodela) in Florida. Bulletin of the Florida State Museum, Biological Sciences 18: 1–100.

MILANOVICH, J. R., D. J. HOCKING, W. E. PETERMAN, AND J. A. CRAWFORD. 2015. Effective use of trails for assessing terrestrial salamander abundance and detection: a case study at Great Smoky Mountains National Park. Natural Areas Journal 35:590–598.

PETRANKA, J. W., AND C. K. SMITH. 2005. A functional analysis of streamside habitat use by southern Appalachian salamanders: implications for riparian forest management. Forest Ecology and Management 210:443–454.

PYRON, R. A., and D. A. Beamer. 2022a. Nomenclatural solutions for diagnosing "cryptic" species using molecular and morphological data facilitate a taxonomic revision of the Black-bellied Salamanders (Urodela, *Desmognathus "quadramaculatus"*) from the southern Appalachian Mountains. Bionomina 27:1–43.

PYRON, R. A., AND D. A. BEAMER. 2022b. Systematics of the Ocoee Salamander (Plethodontidae: *Desmognathus ocoee*), with the description of two new species from the southern Blue Ridge Mountains. Zootaxa 5190:207–240.

PYRON, R. A., K. A. O'CONNELL, E. M. LEMMON, A. R. LEMMON, AND D. A. BEAMER. 2020. Phylogenomic data reveal reticulation and incongruence among mitochondrial candidate species in Dusky Salamanders (*Desmognathus*). Molecular Phylogenetics and Evolution 146:1–13

———. 2022. Candidate-species delimitation in *Desmognathus* salamanders reveals gene flow across lineage boundaries, confounding phylogenetic estimation and clarifying hybrid zones. Ecology and Evolution 12:e8574.

REDMOND, W. H. 1980. Notes on the distribution and ecology of the Black Mountain dusky salamander *Desmognathus welteri* Barbour (Amphibia: Plethodontidae) in Tennessee. Brimleyana 4:123–131.

ROFF, D. A., E. HEIBO, AND L. A. VØLLESTAD. 2006. The importance of growth and mortality costs in the evolution of the optimal life history. Journal of Evolutionary Biology 19:1920–1930.

ROSSELL, C. R., I. C. HAAS, L. A. WILLIAMS, AND S. C. PATCH. 2018. Comparison of relative abundance and microhabitat of *Desmognathus organi* (Northern Pygmy Salamander) and *Desmognathus wrighti* (Southern Pygmy Salamander) in North Carolina. Southeastern Naturalist 17:141–155.

SAEKI, Y., M. TUDA, AND P. H. CROWLEY. 2014. Allocation tradeoffs and life histories: a conceptual and graphical framework. Oikos 123:786–793.

SCHMIDT-NIELSEN, K. 1984. Scaling: Why is Animal Size so Important? Cambridge University Press, UK.

SCHWENK, K., AND D. B. WAKE. 1993. Prey processing in *Leurognathus marmoratus* and the evolution of form and function in desmognathine salamanders (Plethodontidae). Biological Journal of the Linnean Society 49:141–162.

STAUB, N. L. 2016. Age, sexual dimorphism, and growth rates in the Black Salamander, *Aneides flavipunctatus* (Plethodontidae). Copeia 104:52–59.

STEARNS, S. C. 1992. The Evolution of Life Histories. Oxford University Press, UK.

TILLEY, S. G. 1980. Life histories and comparative demography of two salamander populations. Copeia 1980:806–821.

VIEITES, D. R., S. NIETO ROMÁN, M. H. WAKE, AND D. B. WAKE. 2011. A multigenic perspective on phylogenetic relationships in the largest family of salamanders, the Plethodontidae. Molecular Phylogenetics and Evolution 59:623–635.

WAKE, D. B. 2017. Persistent plethodontid themes: species, phylogenies, and biogeography. Herpetologica 73:242–251.

WEAVER, S., D. B. SHEPARD, AND K. H. KOZAK. 2020. Developmental life history is associated with variation in rates of climatic niche evolution in a salamander adaptive radiation. Evolution 74:1804–1814.

WELLS, K. D. 2007. The Ecology and Behavior of Amphibians. University of Chicago Press, USA.

WRIGHT, J., E. B. SOLBU, AND S. ENGEN. 2020. Contrasting patterns of density-dependent selection at different life stages can create more than one fast–slow axis of life-history variation. Ecology and Evolution 10:3068–3078.

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