Life-History Complementarity in the Miniaturized Salamanders Desmognathus aeneus and Desmognathus wrighti

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Life-History Complementarity in the Miniaturized Salamanders *Desmognathus aeneus* and *Desmognathus wrighti*

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This report compares life histories and population ecologies of the miniaturized, terrestrial salamanders *Desmognathus aeneus* and *Desmognathus wrighti* in the southern Nantahala Mountains of southwestern North Carolina. The evaluation is a revision and extension of earlier studies of the species. The earlier field studies were carried out mainly from 1998 to 2001, with additional data collection through 2017. Growth curves and static life tables have been constructed from the earlier datasets. The life tables are snapshots of the population status of the two species during the sampling interval. I have included in the life tables columns that are based on parental and offspring body mass, in addition to the traditional columns based on number of individuals. It is assumed that the populations were in steady state during the sampling phases, under the premise of the equal fitness paradigm (EFP). The presence of a third species of *Desmognathus*, *D. ocoee*, in the forest habitats of the Nantahalas is seen as a complicating factor influencing the interaction of *D. aeneus* and *D. wrighti*. The results are discussed in the context of complementarity wherein two or more similar species having similar resource requirements reduce competition and persist together through differences in life-history strategies.

THE life histories of organisms encompass many rate phenomena, including survival/mortality, growth, development, and reproduction. Differences in such traits can be accommodated under a fast–slow continuum referred to as the "pace-of-life syndrome" or POLS (Wright et al., 2019; Vasilieva, 2022). Thus, fast types at one end of the continuum exhibit rapid growth, early reproduction, many offspring, and short generation time, whereas slow types at the other end grow slowly, reproduce later in life, produce fewer offspring, and have lengthier generations. However, the pattern varies, especially in age- or stage-structured species in which successive stages are subjected to different environmental influences and population regulatory factors. This can promote the evolution of species with fast selection on adult reproduction and slow selection on offspring survival, as well as the reverse (Wright et al., 2020).

Generally, variation in rates of growth and development is associated with variation in metabolic rate (Healy et al., 2019; Burger et al., 2021). The diversity in life histories in animals (and other organisms) reflects the application of scaling laws to variation in metabolic rate, body mass, and generation time (Calder, 1984; Schmidt-Nielsen, 1984; Brown et al., 2022). The correlation between life-history mode and metabolic rate has been expressed in a life-history model referred to as the equal fitness paradigm or EFP, wherein species in an assemblage are considered to have equal fitness (Burger et al., 2021; Brown et al., 2022). It is a postulate of the EFP that most populations are demographically stable and in energy balance much of the time, such that an average parent replaces itself in energy content and biomass with a single surviving, reproducing offspring. Under these conditions, birth rate (b) = death rate (d), intrinsic rate of increase (r) = 0, population growth rate ($dN/dt = rN = 0$), and the net reproductive rate (R_0) = 1.0. Expansion of the model to the metapopulation level would require incorporation of immigration and emigration parameters into the equations (e.g., Vandermeer and Goldberg, 2013: p. 142–148).

In two recent demographic studies of salamanders of the genus *Desmognathus*, I reported that six species in two assemblages in the Cowee and Nantahala Mountains of North Carolina lie at the slow end of the fast–slow continuum of the pace-of-life syndrome, in comparison with animals of similar size (Bruce, 2022, 2023). The studies were conducted under the provisions of the EFP. The findings applied to the two smallest and most terrestrial species in the assemblages, *D. aeneus* and *D. wrighti*. Although the growth and development components of the demographics for the other four species were derived in part from skeletochronological age data, such data were not available for *D. aeneus* and *D. wrighti*, and growth and development of these species were evaluated from frequency distributions of body size (Hining and Bruce, 2005; Bruce, 2009). The latter two studies were based on samples taken in the southern Nantahala Mountains, mainly in March and April, 1998, supplemented by small samples taken in the same months of 2000 and 2001. I continued sampling *D. aeneus* and *D. wrighti* through 2017 in order to obtain data on body mass and to augment existing life-history data of the species (Bruce, 2013, 2014, 2018).

As a requisite for generating life tables, I am assuming that these populations of *D. aeneus* and *D. wrighti* were each in stable demographic equilibrium ($r = 0$, $R_0 = 1.0$) during the period of study. Evidence of steady-state populations in *Desmognathus* in the southern Nantahalas was provided in a long-term study at Coweeta Hydrologic Laboratory from 1972 to 1993. Counts of four species, including *D. aeneus* (but not *D. wrighti*) were made at a single site under a standardized protocol (Hairston and Wiley, 1993; Hairston, 1996). Although sample sizes of *D. aeneus* in each count were small (0–20), no long-term trend was observed, suggesting to the authors a stable equilibrium or attractor in population density. Annual fluctuations in the counts were attributed to weather and year-to-year differences among successive ten-student classes that conducted the counts. The authors reported similar results for the other three species. The years covered by these projects overlapped part of the period of my

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Fig. 1. Southern Nantahala Mountain species of *Desmognathus* discussed in this report. (A, B) *D. wrighti*, adults. (C) *D. aeneus*, adult. (D, E) *D. ocoee*, small individuals, both within the size range of adult *D. aeneus* and *D. wrighti*.

earlier studies of *D. aeneus* and *D. wrighti* in the Nantahalas. Although the Coweeta Creek and upper Nantahala River watersheds have had significant human impacts, the area retains large, relatively-undisturbed forested tracts that support an abundance of plethodontid salamanders.

In the Nantahala Mountains *D. aeneus* and *D. wrighti* are extremely similar in body size, morphology, life history, and habitat utilization (Hining and Bruce, 2005; Bruce, 2009, 2019). This suggests that they may compete for one or another resource where they co-occur. A neutral model of competition between such a species pair would assume identical resource requirements (Hubbell, 2001; Rosindell et al., 2011). This seems unlikely for even very similar species like *D. aeneus* and *D. wrighti*. It is more likely that complementarity in their life-history strategies, in combination with immigration from nearby "source" populations, may represent the means for their long-term persistence under competition for a common set of resources (Jops and O'Dwyer, 2023). In order to examine the degree of complementarity between them, I have organized known life-history attributes of both species into static life tables and from the life tables have generated metabolic life histories that reset the salamanders' demographics in the currencies of mass and energy (Brown et al., 2022).

A complicating factor is the occurrence of a larger species, the streamside *D. ocoee*, in forest habitats in the zone of overlap of *D. aeneus* and *D. wrighti* (Fig. 1). There are major life-history differences between *D. ocoee* and the latter two species; nevertheless, there are overlaps in body size, habitat use, and presumably food habits that represent sources of interaction between the larger and two smaller species

(Bruce, 2009, 2017, 2019). Thus, I have incorporated into the Discussion an evaluation of the possible influence of this species in the ecologies of *D. aeneus* and *D. wrighti*.

MATERIALS AND METHODS

The demographic evaluations of *D. aeneus* and *D. wrighti* in this study are derived from life-history data generated in several published accounts (Hining and Bruce, 2005; Bruce, 2009, 2013, 2014, 2018). Later studies were focused on habitat utilization of *D. aeneus* and *D. wrighti* (Bruce, 2019). These are all referred to as source publications.

Field work was conducted in two adjacent watersheds in the southern Nantahala Mountains of southwestern North Carolina (Bruce, 2019: fig. 2). To the east, samples of *D. aeneus* and *D. wrighti* were taken in the drainages of Ball Creek and Shope Fork, tributaries of Coweeta Creek, which flows into the Little Tennessee River in Macon County, North Carolina. To the immediate west, sampling was conducted in the upper reaches of the Nantahala River basin and a major tributary, Buck Creek, in Macon and Clay Counties, North Carolina. Following preliminary sampling in 1992–1995 (Bruce, 1996), samples were taken in the watershed of Park Creek, a tributary of the Nantahala River, in 1998–2001 (Hining and Bruce, 2005; Bruce, 2009). The Nantahala River joins the Little Tennessee River at Fontana Lake. *Desmognathus aeneus* was found over an elevational range of 685 to 1325 m. At elevations above 915 m, its distribution overlapped that of *D. wrighti*. Throughout the region, both species co-occurred with *D. amphileucus*, *D. monticola*, and *D. ocoee*. In the Nantahala River watershed,
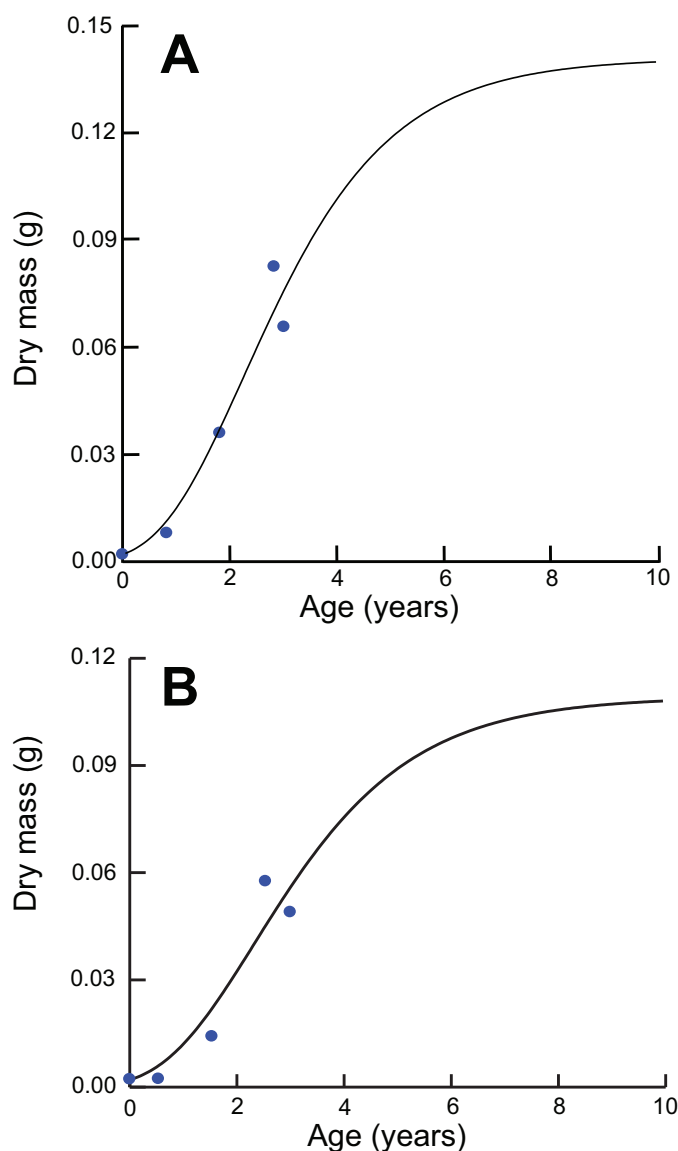
Fig. 2. Provisional growth curves of (A) *Desmognathus aeneus* and (B) *Desmognathus wrighti* fitted by the Gompertz growth function.

both also co-occurred with the aquatic *D. intermedius*. Other plethodontid salamanders in the southern Nantahalas found with *D. aeneus* and *D. wrighti* in the study areas included *Eurycea wilderae*, *Gyrinophilus porphyriticus*,

Pseudotriton ruber, *Hemidactylium scutatum*, *Plethodon shermani*, and *Plethodon shermani* x *P. teyahalee*.

The principal variables provided in the source publications are age (*x*) in years; standard length (*SL*), measured in mm from the tip of the snout to the caudal edge of the cloacal opening on living salamanders; follicle number (*fol*), the count of yolked follicles in the ovaries of gravid females; and dry body mass (*K*), derived from weights of living salamanders (wet mass, *W*) that were recorded to the nearest 0.001 g. Counts of eggs (*egg*) in recently deposited clutches were obtained for *D. aeneus* only.

Because of incomplete data, *D. wrighti* was largely excluded from a later evaluation of reproductive ecology of *D. aeneus* and other desmognathans, which was based on populations at lower elevations (Bruce, 2018). However, I have incorporated the limited data on body size of *D. wrighti* from that study into a $\log_e$-$\log_e$ least-squares regression of wet body mass on standard length, as provided therein for *D. aeneus* (Bruce, 2018: table 1). Given that the energy density of biomass $\approx$ 22.4 kJ/g dry weight and $\approx$ 7 kJ/g wet weight (Burger et al., 2021), I converted wet to dry mass by multiplying wet mass by 0.3125. This provided the means of incorporating values of dry mass into the life table and for estimating parameters of the EFP model. The regression equations are:

$$D.\,aeneus: \ln W = -10.682 + 2.909 \cdot \ln SL \left(n = 98, R^2 = 0.98\right),$$

and

$$D.\,wrighti: \ln W = -10.726 + 2.914 \cdot \ln SL \left(n = 15, R^2 = 0.94\right).$$

Although the sample of *D. wrighti* is small, the equations are nearly identical, the regression lines are nearly coincident, and the R^2 values are high.

I generated growth curves of females of the two species from the output of the MIXDIST analysis of the 1998 samples (Bruce, 2009). Inasmuch as the size distributions of males and females in both species are similar, with similar maxima, I've assumed that growth rates are essentially the same in the two sexes and have used the total dataset to estimate female growth. I included in the dataset estimates of female age and size at first reproduction based on examination of the reproductive organs of the 1998 specimens and dissection of those collected in 2000 and 2001 (Hining and Bruce, 2005). I transformed *SL* values to dry body mass (*K*) from the regressions of ln *W* on ln *SL*, as noted above.

Table 1. Parameters of the equal fitness paradigm (EFP) applied herein to *Desmognathus aeneus* and *Desmognathus wrighti*. Modified from Burger et al. (2019) and Brown et al. (2022). I have substituted the symbols K_O and K_A for M_O and M_A used by Burger et al. (2019) and Bruce (2023), and have reserved *M* for instantaneous mortality rate (Bruce, 2013).

Symbol	Description and units
N_O	Lifetime number of offspring per female at age equal to generation time (G), in years
K_O	Dry mass of an offspring at hatching, in grams
K_A	Dry mass of an adult female at age equal to G, in grams
μ	Relative offspring mass, K_O/K_A
I	$N_O K_O$, parental investment in offspring in one generation, in grams
H	$(K_A - K_O)$, individual growth, in grams
L	Lifetime reproductive investment, $N_O \mu$
P	Individual biomass production, $(1 - \mu) + L$
F	Fraction of cohort production transferred to surviving offspring that reproduce and replace their parents
D_{mor}	Biomass of offspring that die before maturing, in grams

Table 2. Gompertz growth equations for female *Desmognathus aeneus*, *Desmognathus wrighti*, and *Desmognathus ocoee*. $K_x = K_0 exp((\beta/\alpha)(1-exp(-\alpha x)))$, where K = dry body mass in grams, K_0 = body mass at hatching, and x = age in years. The growth curves of *D. aeneus* and *D. wrighti* were derived from the 1998–2001 Park Creek samples (Hining and Bruce, 2005; Bruce, 2009); and that of *D. ocoee* from the female sample of the skeletochronological data set referenced in Bruce (2016a).

Species	K_0	Gompertz parameters		K_∞	95% confidence limits		R^2
		β	α		β	α	
D. aeneus	0.00201	2.72339	0.64080	0.14091	0.29882	−0.24243	0.946
					5.14796	1.52403	
D. wrighti	0.00199	2.38765	0.59615	0.10921	−0.71383	−0.67834	0.901
					5.48912	1.87064	
D. ocoee	0.00475	2.21381	0.45560	0.61272	1.95057	0.37924	0.930
					2.47705	0.53195	

Gompertz growth curves, as described in Panik (2014), were constructed for body mass according to $K_x = K_0 \cdot exp((\beta/\alpha) \cdot (1-exp(-\alpha \cdot x)))$. The Gompertz curve is sigmoidal with an inflection at $d^2K/dx^2 = 0$, representing the maximum rate of growth at age $x = \ln(\beta/\alpha)/\alpha$. I estimated asymptotic values of K as $K_\infty = K_0 \cdot exp(\beta/\alpha)$. On the basis of these estimates, I projected each growth curve beyond the age range represented in the dataset, to age ten years. I justified this approach based on concordant asymptotic values generated by the growth equations, as reported below. Each growth curve incorporates what is a highly variable trait as shown by the *SL* distributions into a single metric that provided a useful framework for comparing metabolic life histories of *D. aeneus* and *D. wrighti*.

Dividing the first derivative of the Gompertz function by body size (dry body mass, K) provides an expression of relative growth rate,

$$\gamma_K = (dK_x/dx)/K_x = \beta \cdot exp(-\alpha x).$$

A logarithmic transformation yields the linear equation

$$\ln(\gamma_K) = \ln(\beta) - (\alpha x),$$

as described in Bruce (2016a). I derived relative growth rates for *D. aeneus* and *D. wrighti* from the Gompertz growth equations. For comparison with Coweeta *D. ocoee*, I have generated absolute and relative growth rates of "females" of the latter that are based on samples of small unsexed juveniles and immature and mature females in the skeletochronological data sets referred to in Bruce (2016a, 2016b).

The life tables are refinements and extensions of the demographics reported in Bruce (2013). In the earlier analysis, I assumed that annual fecundity of *D. aeneus* and *D. wrighti* was constant over the female life span and used the mean follicle count divided by 2 to estimate the m_x values, representing female eggs/female and assuming an equal number of male and female eggs. I necessarily followed this procedure herein for *D. wrighti*. However, for *D. aeneus*, an enhanced sample of gravid females (Bruce, 2018) provided the means for generating age-specific m_x values, i.e., $m_x = (a[SL]^b)/2$. Survival to age x is defined as $l_x = exp(-M \cdot x)$, where M = instantaneous mortality rate. I iterated values of M in order that $\Sigma l_x m_x$ (R_0) equaled 1.0, under the premise noted above that the populations were in a steady state during the period of study. I then multiplied each $l_x m_x$ value by age (x) and took the sum as an estimate of generation time (G) in years.

For *D. aeneus,* I compared the follicle counts with number of eggs in newly deposited clutches attended by the female parent. This was not possible for *D. wrighti*; thus, in constructing life tables, for comparison, I generated m_x columns of both species from the follicle data.

I have expanded the life tables to provide for an accounting of mass/energy balance over the course of the life span, represented by the following parameters: K_x = dry body mass at age x, $b_x = K_0 m_x$ = brood mass of the female component of the brood at age x, $l_x b_x$ = survival probability of the mass of the female component of the brood at age x.

The EFP parameters defined in Table 1 were estimated from the values in the life tables. The parameter F was derived for the female component of the population, wherein fecundity (m_x) is listed as female offspring/female. The elements of the equation of F are fractional values based on the l_x columns of the life tables and applied to the estimates of body mass (K_x). Thus, $F = l_A K_A/(l_A K_A + D_{mor})$, and $D_{mor} = \sum_{x=0}^{x=G} K_X d_X$, where K_x = biomass and d_x = fraction dying before maturing. A is age equal to generation time (G), equal to four years in both species.

Statistics were evaluated with SYSTAT 13.2 (SYSTAT Software, Inc., San Jose, CA).

RESULTS

Males and females of both *D. aeneus* and *D. wrighti* attained similar maximum values of *SL*: *D. wrighti*, 26 mm (males), 27 mm (females); *D. aeneus*, 28 mm (males), 28 mm (females) in the Park Creek 1998–2001 samples (Hining and Bruce, 2005). The other samples included a 30.2 mm female of *D. wrighti* and a 29.3 mm female and 29.8 mm male of *D. aeneus*. Thus, maximum sizes of the two species were nearly identical. Although males of both species mature in their second or third years and females in their third year, there are no obvious differences in growth. I have assumed that the two sexes have similar growth patterns and have not attempted to derive separate female growth curves of either species. It appears that females of both *D. aeneus* and *D. wrighti* usually oviposit initially at three years (Hining and Bruce, 2005; Bruce, 2009). The Gompertz curves for growth in dry body mass of the two species were similar in form and magnitude (Fig. 2), and the estimated parameters of the growth equations were similar (Table 2). The asymptotic values were slightly higher than the maximum body sizes recorded in the 1998–2001 samples (Hining and Bruce, 2005), which lent confidence in their reliability as predictors of age-specific body size. As noted above, slightly larger
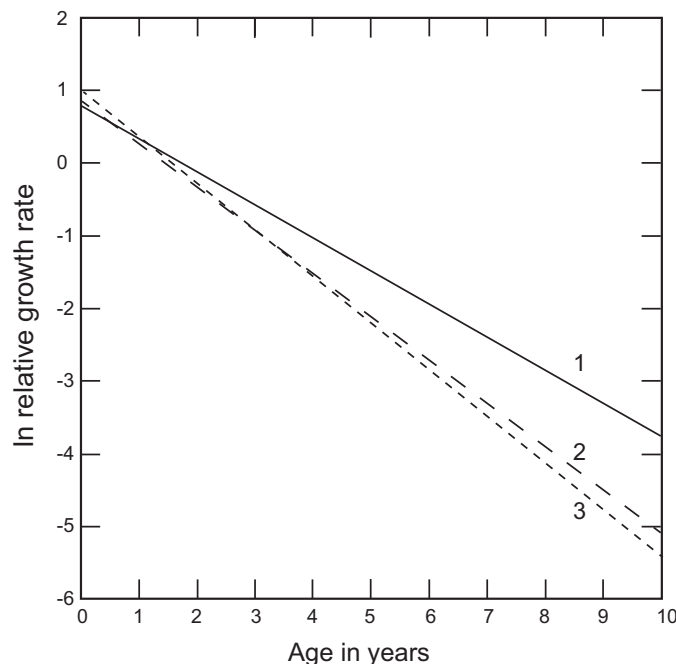
Fig. 3. Decline in relative growth rate (γ_K) with age (x) in three species of *Desmognathus* in the southern Nantahala Mountains. 1. *D. ocoee*, ln (γ_K) = *0.7947–0.4556x*. 2. *D. wrighti*, ln(γ_K) = *0.8703–0.5961x*. 3. *D. aeneus*, ln(γ_K) = *1.0019–0.6408x*.

individuals of both species were observed in the samples from other localities in the Nantahalas. The maximum growth rates in dry mass [($ln\ \beta/\alpha)/\alpha$] were estimated to occur at 2.33 yr (*D. wrighti*) and 2.25 yr (*D. aeneus*), i.e., during the third year, within the age range when males are maturing and when females are yolking their first egg clutches.

Variation in rates of decline in relative growth rate are specified by differences in the Gompertz growth rate parameter, α (Table 2). The decline in rate over ages zero to ten years is essentially identical in *D. aeneus* and *D. wrighti*, and greater than in *D. ocoee* (Fig. 3). Thus, the higher absolute growth rate in *D. ocoee* versus both *D. aeneus* and *D. wrighti* translates into faster declines in relative growth rates in the latter two species.

To determine m_x values of *D. aeneus*, I re-examined the regression of *ln fol* on *ln SL* in Bruce (2014: table 3). A more detailed plot is provided in Figure 4. The sample is small ($n = 16$) and the residual variation is considerable. The regression coefficient ($b = 1.754$) is significant at $\alpha = 0.05$ ($P = 0.012$). Elimination of the single outlier (*SL* = 24.6, *fol* = 8) yielded a marginally significant regression coefficient ($b = 1.29$, $P = 0.027$). However, I retained the full set of fecundity data in predicting the m_x values. The latter are based on *fol/2*, representing female eggs/female, on the assumption of a 1:1 sex ratio of offspring. The more limited data set of fecundity available for *D. wrighti* provided no information on a correlation with female body size. Thus, I based the m_x values on the mean value of *fol/2*.

In *D. aeneus*, follicle numbers (*fol*) in gravid females were greater than egg numbers (*egg*) in 11 deposited clutches of nesting females (mean ± SD: 13.1 ± 2.41 vs. 10.4 ± 1.50). ANCOVA detected no significant effect at $\alpha = 0.05$ for a treatment x covariate (*ln SL*) interaction ($F = 0.284$, df = 1,23, $P = 0.59$), but a significant difference between follicle number and egg number ($F = 6.707$, df = 1,24, $P = 0.016$).

In constructing the life tables of *D. aeneus* and *D. wrighti*, I assumed that females reproduce annually, beginning at three years, and I extended the life spans to ten years (Table 3). Given the small number of follicle counts for *D. wrighti*, the life table of *D. aeneus* is probably more reliable, yet the estimates of the key demographic parameters are very similar. Iteration of the l_x values provided values of the $l_x m_x$ columns that summed to $R_0 = 1.0$. These generated instantaneous mortality rates of $M = 0.796$ (*D. aeneus*) and $M = 0.728$ (*D. wrighti*). Generation times were 4.0 yr for *D. aeneus* and 3.93 yr for *D. wrighti*. I incorporated body mass (K) estimates into the life tables, and generated columns in each illustrating (1) the mass of the female component of the brood (b_x), and (2) the survival component ($l_x b_x$), which adds to the mass of a single hatchling, equivalent to $R_0 = 1.0$.

Based on the updated body-size evaluations of *D. wrighti* and the adjustments in other demographics of both species, estimates of the body-mass parameters have been revised over those listed previously (Table 4, compare with Bruce, 2023: table 4). Their values were calculated directly from the data in the life tables. Adult female mass (K_A) at an age equal to generation time is higher in *D. aeneus* than in *D. wrighti*, consequences of a slightly longer generation time in the former and the difference in growth rate. Given that hatching sizes (K_0) are essentially identical, relative offspring size (μ) is higher in *D. wrighti*. Lifetime reproductive investment of females per unit of female mass (L) appears to be slightly greater in *D. wrighti*, an effect of the higher value of μ in this species. However, the difference also reflects a deficiency in the sample of gravid females of *D. wrighti*, which I was unable to resolve. Total female productivity (P), equal to individual growth ($H = K_A–K_0$) plus investment in offspring ($N_0 K_0$) and normalized to K_A, is nearly equivalent in the two species, as is the fraction of production passed on to offspring that survive and reproduce (F).

DISCUSSION

In a comprehensive study of the life history of *D. aeneus*, Harrison (1967) reported that females reproduce annually starting at an age of three years. He noted that females usually nest under moss cushions near streams, a finding supported by others (Jones, 1981; Marks and Collazo, 1998). These several investigators estimated a mid- to late-spring oviposition season followed by hatching from late spring to mid-summer in the southern Blue Ridge. Data on reproduction in *D. wrighti* are scarce, although females of its sister species, *D. organi*, are known to nest in late summer or autumn, usually in the saturated banks of springheads (Organ, 1961a; Lattea et al., 2016), which represent winter habitat for the population as a whole (Organ, 1961a, 1961b). This pattern probably applies to *D. wrighti* as well (Bruce, 1977; Bernardo, 2000). In the Great Smoky Mountains, females of *D. wrighti* appear to reproduce annually at lower and biennially at higher elevations (Kessler et al., 2024). All of these reports reinforce my interpretation of reproductive ecology of *D. aeneus* and *D. wrighti* (Hining and Bruce, 2005; Bruce, 2009), and justify the incorporation of annual female reproductive schedules in the life tables.

Static life tables like those generated for *D. aeneus* and *D. wrighti* have a provisional status given the premise that the populations are in a steady state ($R_0 = 1.0$). However, if the premise is correct, then the life tables allow a comparison of the demographics of the populations in question, which is

Table 3. Life tables of *Desmognathus aeneus* and *Desmognathus wrighti* generated from the 1998–2001 Park Creek samples (Hining and Bruce, 2005; Bruce, 2009).

D. aeneus

Age (x)	SL (mm)	K (g)	l_x	m_x	$l_x m_x$	$x l_x m_x$	b_x	$l_x b_x$
0	6.94	0.00201	1.0					
1	13.85	0.01501	0.45090					
2	19.94	0.04331	0.20332					
3	24.16	0.07568	0.09168	5.41	0.496	1.489	0.011	0.000998
4	26.73	0.10156	0.04134	6.46	0.267	1.069	0.013	0.000537
5	28.19	0.11858	0.01864	7.10	0.132	0.661	0.014	0.000266
6	28.99	0.12867	0.00840	7.46	0.063	0.376	0.015	0.000126
7	29.43	0.13432	0.00379	7.65	0.029	0.203	0.015	0.000058
8	29.66	0.13740	0.00171	7.76	0.013	0.106	0.016	0.000027
9	29.78	0.13905	0.00077	7.81	0.006	0.054	0.016	0.000012
10	29.84	0.13993	0.00035	7.84	0.003	0.027	0.016	0.000005
Sum					1.01	3.99		0.00203

D. wrighti

Age (x)	SL (mm)	K (g)	l_x	m_x	$l_x m_x$	$x l_x m_x$	b_x	$l_x b_x$
0	7.00	0.00199	1.0					
1	12.97	0.01202	0.48300					
2	18.23	0.03238	0.23329					
3	21.98	0.05590	0.11268	4.625	0.521	1.56	0.0092	0.001039
4	24.37	0.07551	0.05443	4.625	0.252	1.01	0.0092	0.000502
5	25.79	0.08912	0.02629	4.625	0.122	0.608	0.0092	0.000242
6	26.61	0.09764	0.01270	4.625	0.059	0.352	0.0092	0.000117
7	27.08	0.10267	0.00613	4.625	0.028	0.199	0.0092	0.000056
8	27.33	0.10556	0.00296	4.625	0.014	0.110	0.0092	0.000027
9	27.48	0.10718	0.00143	4.625	0.007	0.060	0.0092	0.000013
10	27.56	0.10809	0.00069	4.625	0.003	0.032	0.0092	0.000006
Sum					1.0	3.93		0.00200
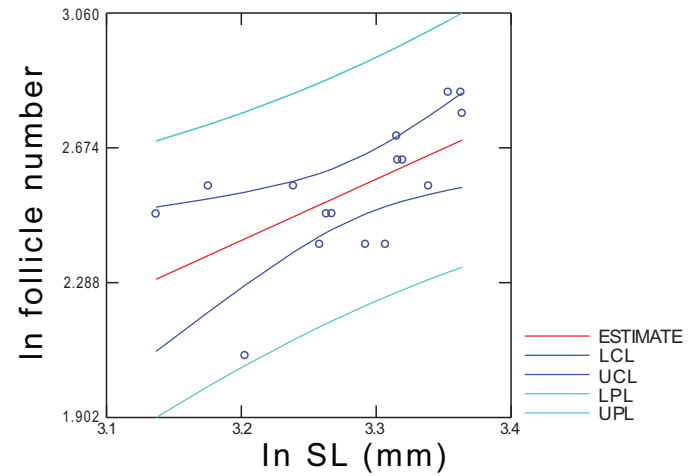
Fig. 4. Least-squares regression of ln follicle number on ln standard length for southern Nantahala females of *Desmognathus aeneus*. The least-squares regression equation is *ln fol = −3.205 + 1.754·ln SL* (Bruce, 2014). LCL, UCL: lower, upper 95% confidence limits. LPL, UPL: lower, upper prediction limits.

applicable at least for the period (spring 1998) when the samples were taken. But the life tables may have broader applicability based on the results of the later life-history studies (Bruce, 2013, 2014, 2018). As evaluated herein, the demographics and life histories of the two species are similar in respect to individual growth, body-size traits, age at first reproduction, generation time, and survivorship. In expanding the evaluations to examine metabolic life histories, I found that *D. aeneus* and *D. wrighti* appear to follow similar pathways relative to energy acquisition and distribution. The values of the biomass productivity parameters (*P*, *F*) fall at the high end of the range reported for animals (Brown et al., 2022). This supports my contention that the two species (and other desmognathans) lie at the slow end of the fast–slow axis of life-history variation in animals (Bruce, 2023).

The difference in fecundity between the species is considered, at least in part, a deficiency in the dataset for *D. wrighti*. The body size–fecundity relationship in Nantahala *D. aeneus* is similar to that reported for the species by Harrison (1967: fig. 1), taking into account the latter's procedure of measuring standard length to the anterior end of the vent on preserved specimens. The difference reported here between number of ovarian follicles and those of eggs in field clutches suggests a tendency for *D. aeneus* to oviposit fewer than the full complement of yolked follicles. However, in evaluating larger samples, Harrison (1967: table 2) found a smaller difference between mean numbers of follicles (11.7) and deposited eggs (10.7) than in the Nantahala samples of this study; the difference is marginally non-significant at α = 0.05.

Ecological and life-history similarities suggest that co-occurring members of the two species may compete for one or more shared resources, including habitat features of moist woodlands, especially cover objects, and food, mainly small arthropods like mites, spiders, collembolans, dipterans, and coleopterans (Bruce, 2009, 2019). Foods of *D. aeneus* have been documented by Donavan and Folkerts (1972) and Jones (1981); those of *D. wrighti* are undocumented but have been recorded for its close relative, *D. organi* (Hairston, 1949). Mosses, which harbor a variety of small arthropods, are

Table 4. Elements of metabolic life histories of *Desmognathus aeneus* and *Desmognathus wrighti*. The symbols are defined in Table 1. The values of the parameters are derived from the life tables in Table 3.

Species	K_O	K_A	μ	N_O	I	H	L	P	F
D. aeneus	0.00201	0.10134	0.0198	23.73	0.0477	0.0993	0.4699	1.450	0.162
D. wrighti	0.00199	0.07433	0.0268	18.34	0.0365	0.0723	0.4915	1.465	0.191

important habitats of Nantahala *D. aeneus* (especially) and *D. wrighti* (Bruce, 2019). The long-term persistence of the species in the area of co-occurrence in the Nantahala Mountains under a regime of competition would seemingly require some differences in resource utilization and life history. Differences between the species include phenology (schedule of nesting), nesting habitat, and behavior (Hining and Bruce, 2005; Bruce, 2009). In my experience, *D. wrighti* is a more active salamander than *D. aeneus*; it jumps and has a greater proclivity for climbing on vegetation (see Hairston, 1987: p. 186–187).

The long-term persistence of similar species that share resources and maintain similar effective population sizes is termed complementarity (Jops and O'Dwyer, 2023). The latter authors have defined effective population size as a function of reproductive rate, generation time, and variance in individual lifetime reproductive success (see their equation 1). As they noted, it is expected that such species have evolved differences in one or more critical aspects of reproductive strategy that allow coexistence. It is a condition of the Jops and O'Dwyer (2023) complementarity model that effective population sizes of the competing species are equivalent or nearly so. In the particular case of *D. aeneus* and *D. wrighti* in the southern Nantahalas, some local populations may have been approximately equal in effective size, e.g., those at Park Creek (Hining and Bruce, 2005).

The zone of overlap of *D. aeneus* and *D. wrighti* extends from approximately 900 m to 1,325 m in elevation. The former species occurs down to the lowest elevation surveyed, at 685 m. The upper limits are not well defined, but possibly *D. wrighti* extends upward to the highest summit (1,676 m) at Standing Indian Mountain. The aforementioned differences in life histories and ecologies may express complementary of the two species in the zone of overlap at mid-elevations in the cool and moist environment of the southern Nantahala Mountains. Immigration could also contribute to their persistence over the long term, but I have not attempted to modify the EFP model to account for metapopulation dynamics.

Desmognathus ocoee occurs throughout the woodlands occupied by *D. aeneus* and *D. wrighti* and shares habitat and probably food resources with the latter two species (Hining and Bruce, 2005; Bruce, 2009). It is a larger species and has a biphasic life cycle that features a relatively brief larval phase. Males and females are larger and about one year older at sexual maturation than their counterparts among *D. aeneus* and *D. wrighti* (Bruce, 2009, 2017). Females of *D. ocoee* nest later in the year (mid-summer) than *D. aeneus*, often under moss like *D. aeneus*, but close to the streambank since their hatchling larvae must crawl down to water. However, on 28 July 2013, I observed an adult *D. aeneus* attending a clutch of late embryos under moss on the bank of a seepage close to a clutch of early embryos of *D. ocoee* attended by an adult. Several other nesting *D. ocoee* were observed nearby under moss along the same seep.

Competition between *D. ocoee* and either *D. aeneus* or *D. wrighti* is probably most likely between juveniles of the former species and juveniles/adults of the latter two, which overlap broadly in size (Bruce, 2009). Although Hairston (1986) found no evidence of competition between *D. ocoee* and *D. aeneus* in the Nantahalas, his study plots extended only 7 meters from the stream edge. (*Desmognathus wrighti* was not found on Hairston's plots, which were located at lower elevations.)

Absolute and relative growth rates are higher in *D. ocoee* than in either *D. aeneus* or *D. wrighti*. This means that adults of the latter two species are exposed to interaction with similar-sized *D. ocoee* throughout their lives, whereas *D. ocoee*, especially females, generally exceed *D. aeneus* and *D. wrighti* in body size during their reproductive years (Bruce, 2009). These relations may apply to populations of *D. aeneus* and *D. wrighti* (and *D. organi*) in other areas where they co-occur with other small streamside desmognathans. In the Great Smoky Mountains, Rossell et al. (2018) proposed that *D. wrighti* select smaller cover objects in order to reduce encounters with larger salamanders, including *D. adatsihi* and *D. imitator*.

The life tables of *D. aeneus* and *D. wrighti* were derived mainly from the data of the 1998–2001 samples, under the premise of the steady-state EFP model. Concerns about declining amphibian populations (Luedtke et al., 2023; Nowakowski et al., 2023) raise uncertainties about the current applicability of the EFP model. In any case, elucidation of a more realistic construct of the population dynamics of the two species will require long-term, manipulative field experiments of *D. aeneus* and *D. wrighti*, as noted by Hining and Bruce (2005), and including *D. ocoee* as well.

DATA ACCESSIBILITY

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LITERATURE CITED

Bernardo, J. 2000. Early life histories of dusky salamanders, *Desmognathus imitator* and *D. wrighti*, in a headwater seepage in Great Smoky Mountains National Park, USA. Amphibia-Reptilia 21:403–407.

Brown, J. H., J. R. Burger, C. Hou, and C. A. S. Hall. 2022. The pace of life: metabolic energy, biological time, and life history. Integrative and Comparative Biology 62:1479–1491.

Bruce, R. C. 1977. The Pygmy Salamander, *Desmognathus wrighti* (Amphibia, Urodela, Plethodontidae), in the Cowee Mountains, North Carolina. Journal of Herpetology 11:246–247.

Bruce, R. C. 1996. Life-history perspective of adaptive radiation in desmognathine salamanders. Copeia 1996:783—790.

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

Bruce, R. C. 2013. Size-mediated tradeoffs in life-history traits in dusky salamanders. Copeia 2013:262–267.

Bruce, R. C. 2014. Reproductive allometry in three species of dusky salamanders. Copeia 2014:419–427.

Bruce, R. C. 2016a. Relative growth rates in three species of *Desmognathus* (Amphibia: Plethodontidae). Herpetologica 72:174–180.

Bruce, R. C. 2016b. Application of the Gompertz function in studies of growth in dusky salamanders (Plethodontidae: *Desmognathus*). Copeia 104:94–100.

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

Bruce, R. C. 2018. Interspecific variation in reproductive effort in two assemblages of dusky salamanders. Journal of Herpetology 52:209–214.

Bruce, R. C. 2019. Life history evolution in plethodontid salamanders and the evolutionary ecology of direct development in dusky salamanders (*Desmognathus*). Herpetological Review 50:673–682.

Bruce, R. C. 2022. Size and cycle in dusky salamanders. Journal of Herpetology 56:444–453.

Bruce, R. C. 2023. Pace-of-life in dusky salamanders. Herpetologica 79:119–127.

Burger, J. R., C. Hou, and J. H. Brown. 2019. Toward a metabolic theory of life history. Proceedings of the National Academy of Sciences of the United States of America 116:26653–26661.

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, Cambridge, Massachusetts.

Donavan, L. A., and G. W. Folkerts. 1972. Foods of the Seepage Salamander, *Desmognathus aeneus* Brown and Bishop. Herpetologica 28:35–37.

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

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

Hairston, N. G., Sr. 1987. Community Ecology and Salamander Guilds. Cambridge University Press, Cambridge, UK.

Hairston, N. G., Sr. 1996. Predation and competition in salamander communities, p. 161–189. *In*: Long-Term Studies of Vertebrate Communities. M. L. Cody and J. A. Smallwood (eds.). Academic Press, New York.

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.

Harrison, J. R. 1967. Observations on the life history, ecology and distribution of *Desmognathus aeneus aeneus* Brown and Bishop. American Midland Naturalist 77:356–370.

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.

Hubbell, S. P. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton, New Jersey.

Jones, R. L. 1981. Distribution and ecology of the Seepage Salamander *Desmognathus aeneus* Brown and Bishop (Amphibia: Plethodontidae), in Tennessee. Brimleyana 7:95–100.

Jops, K., and J. P. O'Dwyer. 2023. Life history complementarity and the maintenance of biodiversity. Nature 618:986–991.

Kessler, E. J., J. A. Crawford, W. E. Peterman, and D. J. Hocking. 2024. Reproductive ecology of Southern Pygmy Salamanders (*Desmognathus wrighti*) along an elevational gradient. Herpetologica 80:117–123.

Lattea, W., T. W. Pierson, and E. T. Carter. 2016. *Desmognathus organi* (northern pygmy salamander): nest. Herpetological Review 47:100–101.

Luedtke, J. A., J. Chanson, K. Neam, L. Hobin, A. O. Marciel, A. Catenazzi, A. Borzée, A. Hamidy, A. Aowphol, A. Jean, A. Sosa-Bartuano, A. Fong G., A. de Silva, A. Fouquet . . . S. N. Stuart. 2023. Ongoing declines for the world's amphibians in the face of emerging threats. Nature 622:308–314.

Marks, S. B., and A. Collazo. 1998. Direct development in *Desmognathus aeneus* (Caudata: Plethodontidae): a staging table. Copeia 1998:637–648.

Nowakowski, A. J., J. I. Watling, A. Murray, J. L. Deichmann, T. S. Akre, C. L. Muñoz Brenes, B. T. Todd, L. McRae, R. Freeman, and L. O. Frischkoff. 2023. Protected areas slow declines unevenly across the tetrapod tree of life. Nature 622:101–106.

Organ, J. A. 1961a. Life history of the Pygmy Salamander, *Desmognathus wrighti*, in Virginia. American Midland Naturalist 66:384–390.

Organ, J. A. 1961b. Studies of the local distribution, life history, and population dynamics of the salamander genus *Desmognathus* in Virginia. Ecological Monographs 31:189–220.

Panik, M. J. 2014. Growth Curve Modeling: Theory and Applications. John Wiley & Sons, Inc., Hoboken, New Jersey.

Rosindell, J., S. P. Hubbell, and R. S. Etienne. 2011. The unified neutral theory of biodiversity and biogeography at age ten. Trends in Ecology and Evolution 26:340–348.

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.

Schmidt-Nielsen, K. 1984. Scaling: Why Is Animal Size so Important? Cambridge University Press, Cambridge, UK.

Vandermeer, J. H., and D. E. Goldberg. 2013. Population Ecology: First Principles. Princeton University Press, Princeton, New Jersey.

Vasilieva, N. A. 2022. Pace-of-life syndrome (POLS): evolution of the concept. Biology Bulletin 49:750–762.

Wright, J., G. H. Bolstad, Y. G. Araya-Ajoy, and N. J. Dingemanse. 2019. Life-history evolution under fluctuating density-dependent selection and the adaptive alignment of pace-of-life syndromes. Biological Reviews 94:230–247.

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.