

HERPETOLOGICA

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SPECIES OF DUSKY SALAMANDERS
(PLETHODONTIDAE: *DESMOGNATHUS*)

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Published by The Herpetologists' League, Inc.

PROXIMATE CONTRIBUTIONS TO ADULT BODY SIZE IN TWO SPECIES OF DUSKY SALAMANDERS (PLETHODONTIDAE: *DESMOGNATHUS*)

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ABSTRACT: I used skeletochronological data to evaluate the contributions of propagule size, larval/juvenile growth, and age at first reproduction to differences in adult body size in two species of plethodontid salamanders of the genus *Desmognathus*. The traits in question were evaluated in populations of the larger *D. quadramaculatus* and smaller *D. monticola* in the southern Blue Ridge Mountains of North Carolina, USA. Gompertz and von Bertalanffy functions were fitted to the plots of standard length on skeletochronological age of each complete sample (larvae and/or juveniles, and adults) of earlier data sets; linear functions were fitted to data of immatures (larvae and/or juveniles). In order to examine the relationship of body mass and age, I conducted regressions of body mass on standard length in later samples of both species, calculated estimated body masses of the salamanders in the skeletochronological data sets, and then fitted a modified Gompertz function to each plot of body mass on age. The results showed that age at first reproduction is the principal factor contributing to differences between the species in size at first reproduction and adult size. Larger propagule sizes (i.e., hatching sizes) in *D. quadramaculatus* versus *D. monticola* may also be a factor; however, there is no evidence that a difference in larval/juvenile growth rate contributes to the adult size differential. Comparison of two populations of *D. monticola* suggested that small differences in adult body size result mainly from slight differences in age at first reproduction. Tradeoffs among propagule size, clutch size, growth, and age and size at first reproduction are discussed in the context of selective pressures that may have generated diversification in body size and life history in the genus.

Key words: Age; Body size; *Desmognathus*; Growth; Life history; Salamanders

THE 21 SPECIES of the genus *Desmognathus* vary markedly in body size but are morphologically conservative otherwise (Sweet, 1973, 1980). The largest species, *D. quadramaculatus*, attains standard lengths about 4 times greater and body masses about 60 times greater than those of the three smallest species, *D. aeneus*, *D. organi*, and *D. wrighti*. At the southern end of its range in northeastern Georgia, USA, *D. quadramaculatus* reaches standard lengths of 120 mm (Camp et al., 2000). Differences in adult body size in *Desmognathus* are correlated with differences in propagule size and age at first reproduction. Thus, larger species produce larger eggs that yield larger hatchlings than smaller species (Beachy, 1993; Bruce, 2005; Orr and Maple, 1978; Tilley and Bernardo, 1993); and larger species are older at first reproduction than smaller species (Bruce et al., 2002; Castanet et al., 1996; Tilley and Bernardo, 1993). A third obvious factor contributing to size differences in many kinds of organisms is growth rate

(Arendt, 1997). In *Desmognathus* a growth effect is expected to be expressed mainly as variation in larval and juvenile growth rate, given that growth declines in these salamanders upon attainment of sexual maturity (Bruce et al., 2002; Castanet et al., 1996). This relationship has been best studied in the *D. ochrophaeus* complex, and is especially evident in females (Fitzpatrick, 1973; Hom, 1988; Tilley, 1980).

In *Desmognathus* body size is strongly correlated with the adaptive zone of species along the aquatic-to-terrestrial habitat gradient from stream to forest (Hairston, 1987). Thus, with few exceptions, the larger species are more aquatic, with lengthier larval phases, and the smaller are more terrestrial, with briefer larval phases. For example, in the species under study herein, the body-size-habitat association applies to the larger aquatic species, *D. quadramaculatus*, and the smaller streambank form, *D. monticola* (e.g., Hairston, 1980: Tables 1 and 2; Petranka and Smith, 2005: Fig. 3). Such correlations in *Desmognathus* have been posited as outcomes of natural selection in response to interspe-

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TABLE 1.—Summary of estimates of life-history parameters of *Desmognathus* salamanders at Coweeta Creek (Cow) and Wolf Creek (WC) watersheds, North Carolina, USA. Under age at first reproduction, modal numbers, in parentheses, are based on small sample sizes and cannot be estimated for *D. quadramaculatus*. Under hatching, sources are Bruce (1988, 1990; R. C. Bruce, unpublished data) and, for nearby watersheds, Orr and Maple (1978). Data sources for age and size at first reproduction are Bruce (1993), Bruce et al. (2002), Bruce and Hairston (1990), and Castanet et al. (1996).

Species (population)	Age and size at first reproduction					
	Hatching		Males		Females	
	\bar{x} SL (mm)	Median date	Age (yr)	SL (mm)	Age (yr)	SL (mm)
<i>D. monticola</i> (WC)	11.8	15 August	4–5 (5)	46–50	5–7 (6)	49–53
<i>D. monticola</i> (Cow)	11.8	15 August	4–5 (5)	46–57	5–7 (6)	52–59
<i>D. quadramaculatus</i> (Cow)	14.0	1 August	7–8	65–74	9–10	80–84

cific competition and intraguild predation (Bruce, 2008; Table 2; Hairston, 1986, 1996; Kozak et al., 2005). Therefore, if niche differentiation in the genus along the dimensions of body size and habitat utilization is a consequence of interspecific interactions, it has presumably involved selection on some combination of propagule size, growth and differentiation rates, and age at first reproduction.

In this paper I reanalyze skeletochronological data on two of the three species of *Desmognathus* (*D. monticola* and *D. quadramaculatus*) that were studied by Bruce et al. (2002). The third species (*D. ocoee*) has been treated elsewhere (Bruce, 2009). Populations of both species were sampled at a single locality, and one of the species (*D. monticola*) was sampled at a second locality. Although Bruce et al. (2002) fitted Gompertz functions to plots of size against age, they did not examine differences in the size–age relation-

ship between species or populations. However, such an evaluation would seem to be important for identifying the contributions of relevant life-history traits to niche differentiation between the species. Thus, in the present study I have extended the analysis, under the null hypothesis that early growth rates of larvae and juveniles do not differ between *D. monticola* and *D. quadramaculatus*, or between the two populations of *D. monticola*. This hypothesis is evaluated within the framework of known differences in the other two factors that influence body size at first reproduction, namely propagule size and age at first reproduction. Data on these two traits in the populations under consideration, summarized from the literature, are presented in Table 1.

MATERIALS AND METHODS

Samples of *Desmognathus quadramaculatus* and *D. monticola* were collected in 1994–

TABLE 2.—Relationships fitted by the Gompertz and von Bertalanffy functions between body size (standard length [SL] in mm) and age in years in two species of *Desmognathus* from the Coweeta Creek (Cow) and Wolf Creek (WC) watersheds. The 95% confidence limits are given in parentheses for the Gompertz parameters β and α , and the von Bertalanffy parameters k and r . The values of the coefficient of determination (R^2) in this and later tables are adjusted multiple R^2 .

Species	Gompertz parameters				
	SL ₀	β	α	R^2	SL _{max}
<i>D. monticola</i> (WC)	11.8	0.532 (0.494, 0.570)	0.261 (0.224, 0.297)	0.921	90.6
<i>D. monticola</i> (Cow)	11.8	0.642 (0.600, 0.684)	0.333 (0.302, 0.363)	0.920	81.1
<i>D. quadramaculatus</i> (Cow)	14.0	0.489 (0.463, 0.515)	0.243 (0.226, 0.261)	0.942	104.7
Species	von Bertalanffy parameters				
	SL _∞	k	r	R^2	SL ₀
<i>D. monticola</i> (WC)	90.0	0.941 (0.904, 0.978)	0.157 (0.078, 0.236)	0.911	5.3
<i>D. monticola</i> (Cow)	88.1	0.981 (0.926, 1.036)	0.200 (0.149, 0.252)	0.919	1.7
<i>D. quadramaculatus</i> (Cow)	120.0	0.903 (0.880, 0.926)	0.111 (0.084, 0.139)	0.947	11.6

1995 from the Coweeta Creek watershed at Coweeta Hydrologic Laboratory, in the southern Nantahala Mountains, Macon County, North Carolina, USA. A sample of *D. monticola* was taken in 1995 from the Wolf Creek watershed of Cullowhee Mountain, a spur of the Cowee Mountains, Jackson County, North Carolina. The two localities are 35 km apart. Descriptions of the sampling areas are given in Bruce et al. (2002), as is the methodology of the skeletochronological estimation of age in these samples.

Based on growth marks in cross-sections of femurs, Bruce et al. (2002) estimated skeletochronological age to the nearest year. I have refined and extended the earlier analysis, first by recalculating ages in years to the nearest half-month, based on actual sampling dates and estimates of the median hatching date for each population (Table 1). Body size was measured as standard length (SL), taken from the tip of the snout to the posterior end of the cloacal slit on living individuals, and recorded to the nearest 0.1 mm. Numbers of individuals reliably aged by skeletochronology were 106 *D. quadramaculatus* and 111 *D. monticola* from Coweeta, and 85 *D. monticola* from Wolf Creek. The sample of *D. quadramaculatus*, a species having a larval period of 2–4 yr, included both larvae and postmetamorphic individuals, but those of *D. monticola*, wherein the larval period is 8–10 mo, included postmetamorphic individuals only.

Given the absence of individual growth data based on mark–recapture, plots of body size against skeletochronological age provided useful approximations of growth. Inasmuch as the plots of standard length against age were nonlinear, I fitted Gompertz and von Bertalanffy functions to the data. Both models have been used in growth studies of salamanders (e.g., Gompertz by Marvin [2001] and von Bertalanffy by Üzüm and Olgun [2009]). Because larvae and small juveniles were not sexed in the Bruce et al. (2002) study, and because of the relatively small numbers in some of the adult samples, I did not evaluate males and females separately.

In immatures (larvae and/or juveniles) of all three populations, wherein plots of standard length against age were essentially linear, I calculated linear functions and conducted

analyses of covariance (ANCOVAs) of the larval/juvenile regressions of standard length on age, with species or population as the grouping variable, standard length as the dependent variable, and age as the covariate. In the ANCOVA of Coweeta *D. quadramaculatus* and *D. monticola*, the evaluation was restricted to the age range of immature *D. monticola* (to 5 yr); older immature *D. quadramaculatus* were excluded from the analysis, inasmuch as the objective here was to evaluate differences in body size attributable to differences in larval/juvenile growth only.

The Gompertz function generates a sigmoid curve according to the equation, $SL_A = SL_0 \exp\{\frac{\beta}{\alpha}[1 - \exp(-\alpha \times A)]\}$, where SL_A = standard length in mm at age A in years, SL_0 = standard length at hatching (age 0), and β and α are the Gompertz parameters, where β = initial specific growth rate and α = rate of decay of β . Differences between species and populations were evaluated by the 95% confidence intervals of the α and β parameters. The asymptotic size is given by $SL_{max} = SL_0 \exp(\beta/\alpha)$. By taking first and second derivatives of the Gompertz function (see Appendix 1) and setting $d^2SL/dA^2 = 0$, solving for A gives the estimated age at the rate of maximum growth, $A_\lambda = \ln(\beta/\alpha)/\alpha$. Substituting this value into (1) the Gompertz equation and (2) the first derivative gives (1) the size at this age and (2) the maximum value of the growth rate.

The von Bertalanffy equation represents a decaying exponential function, $SL_A = SL_\infty [1 - k \times \exp(-r \times A)]$, where SL_A = standard length in mm at age A in years, SL_∞ = asymptotic standard length, and r = the growth coefficient. k is a parameter related to size at hatching (age 0); thus, $SL_0 = SL_\infty(1 - k)$. The slope of the curve is given by $dSL/dA = SL_\infty \times k \times r \times \exp(-r \times A)$. Under the von Bertalanffy model, the maximum rate of growth occurs at age 0, which is the age at hatching in this application.

Bruce et al. (2002) did not measure body masses of the salamanders aged by skeletochronology. I undertook a preliminary evaluation of the body-mass–age relationship, by determining first the relation of mass and standard length, and then incorporating the parameters estimated by the resulting regres-

sions into a modification of the Gompertz function. For body-mass data, I referred to a sample of *D. monticola* from Wolf Creek taken by me in 1989, in which standard lengths (nearest 0.1 mm) and body mass (M, nearest mg) were taken on living salamanders. Also, John Maerz of the University of Georgia provided a data set of standard lengths (nearest mm) and body masses (nearest mg) of living *D. quadramaculatus* and *D. monticola* taken at Coweeta Hydrologic Laboratory in 2007–2009 for an unrelated project. Additionally, I collected *Desmognathus monticola* ($n = 30$) and *D. quadramaculatus* ($n = 33$) at Coweeta in October–December 2009 from the same watersheds in which the 1994–1995 samples had been taken; the salamanders were anesthetized in MS-222 and measured for standard length (nearest 0.1 mm) and mass (nearest mg). The salamanders were subsequently revived and released at the sampling sites. I fitted linear functions to the log-transformed values in all five mass–length data sets, according to the equation $\ln M = \ln a + b \times \ln SL$, rearranged the equation as $SL = (M/a)^{1/b}$, and equated the latter expression to the Gompertz function, $SL = SL_0 \exp\{[\beta/\alpha][1 - \exp(-\alpha \times A)]\}$. Thus, $M_A = \{a^{1/b} \times SL_0 \exp[(\beta/\alpha)(1 - \exp(-\alpha \times A))]\}^b$. Taking first and second derivatives (see Appendix 1) and solving for $d^2M/dA^2 = 0$ provided an estimate of the age at maximum rate of increase in mass, $A_\lambda = \ln[(b \times \beta)/\alpha]/\alpha$. Again, substituting this value into (1) the Gompertz equation for mass and (2) the first derivative, gives estimates of (1) mass at this age and (2) the maximum value of the growth rate.

Statistics were calculated with SYSTAT v.12. For nonlinear equations fitted by a loss model, differences in fitted parameters between species and populations were evaluated by the 95% confidence intervals. In other statistical tests significance was evaluated at $\alpha = 0.05$.

RESULTS

The Gompertz equations provided good fits to the data of all three populations, with R^2 values ≥ 0.92 (Table 2). The form of the Gompertz plots reflected the tendency for growth in standard length to decline at maturation in these species (Fig. 1). In *D.*

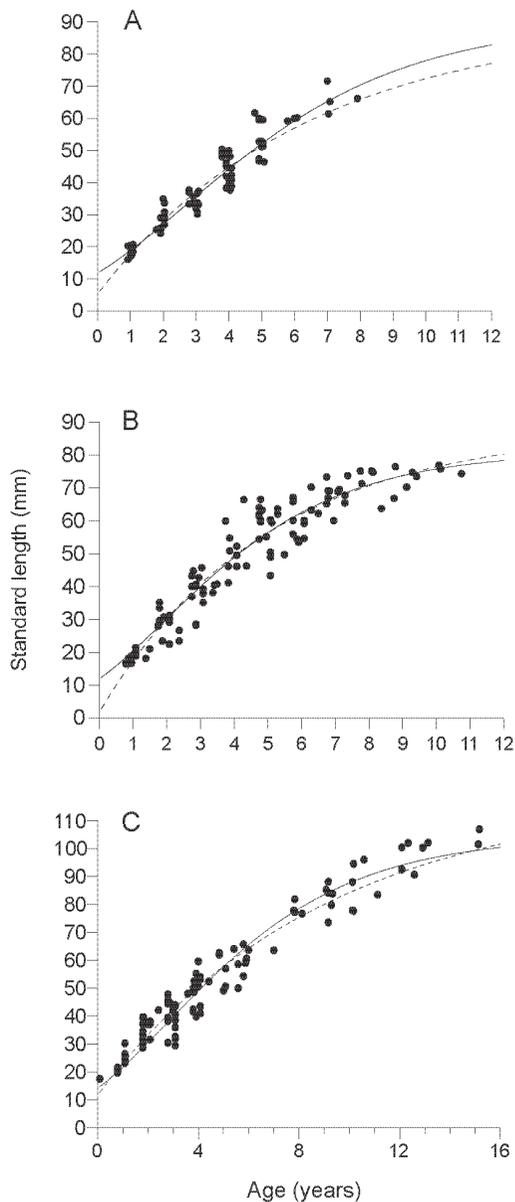
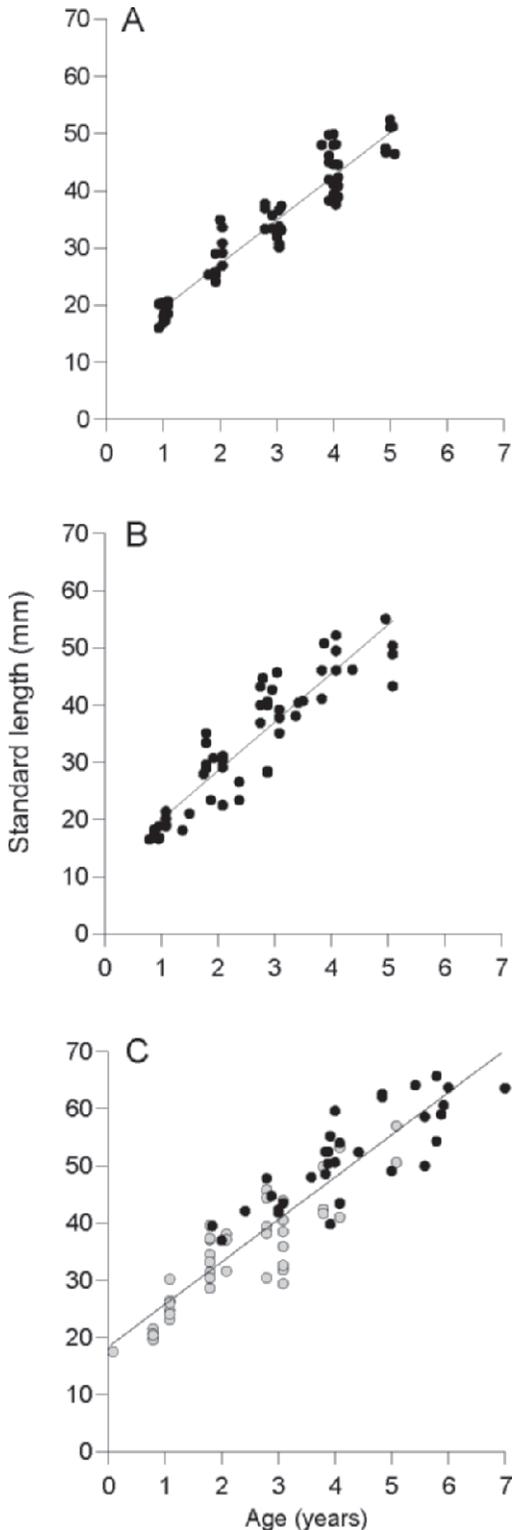


FIG. 1.—Plots of standard length against age for (A) Wolf Creek *Desmognathus monticola*, (B) Coweeta *D. monticola*, and (C) Coweeta *D. quadramaculatus*, fitted by Gompertz (solid curve) and von Bertalanffy (dashed curve) functions. To illustrate the form of the growth functions, the fitted curves for *D. monticola* are extended beyond the range of the data, to 12 yr.

quadramaculatus there was no obvious effect of metamorphosis (i.e., larvae versus postmetamorphic juveniles), and the Gompertz function was fitted to the pooled data of all



life-history stages. The α and β parameters differed significantly between species at Coweeta, as expected for species of very different adult sizes, but also between Coweeta and Wolf Creek *D. monticola* (Table 2). For the two species at Coweeta, the maximum or asymptotic sizes were close to the maxima recorded in the samples; however, that of Wolf Creek *D. monticola* was higher than expected, probably an effect (i.e., sampling bias) of the relatively few older adults in this sample. For each population, the most rapid increase in size occurred during the immature phase of the life cycle, and at an older age and larger size (2.9 yr, 38.5 mm SL) in *D. quadramaculatus* than in either the Coweeta (2.0 yr, 29.8 mm SL) or Wolf Creek (2.7 yr, 33.3 mm SL) population of *D. monticola*. The ratio of size at the age of maximum growth to asymptotic size is fixed by the Gompertz function at $\exp(-1) = 0.368$.

Although the form of the von Bertalanffy plots also tracked the decline in growth with maturation (Fig. 1) and provided adequate fits to the data, this model was less realistic because the values of the intercepts, $SL_0 = SL_{\infty}(1 - k)$, were lower (Table 2) than actual hatching sizes of either species (Table 1). This discrepancy is explained by the exponential form of the von Bertalanffy plot, in contrast to the slight sigmoidal pattern of early growth in these species, which is better accounted for by the Gompertz function.

For immatures, plots of standard length against age were essentially linear in all three populations (Fig. 2), and linear regressions were calculated for individuals ≤ 5.0 yr in *D. monticola* and ≤ 7.0 yr in *D. quadramaculatus*. This excluded a few larger individuals of each species that were scored as immatures, but fell well within the size range of adults. In both populations of *D. monticola* the intercepts were close to hatching sizes; for *D. quadramaculatus* the intercept was greater, probably an effect of the scarcity of very young

←

FIG. 2.—Plots of standard length against age for immature *Desmognathus*, fitted by linear functions. (A) Wolf Creek *Desmognathus monticola* ($n = 69$, $SL = 11.8 + 7.67AGE$, $R^2 = 0.907$). (B) Coweeta *D. monticola* ($n = 58$, $SL = 11.4 + 8.52AGE$, $R^2 = 0.835$). (C) Coweeta *D. quadramaculatus* ($n = 82$, $SL = 18.4 + 7.41AGE$, $R^2 = 0.842$). Shaded circles: larvae, black circles: juveniles.

TABLE 3.—Relationship of body mass (M in g) and standard length (SL in mm) according to the power function, $M = a \times SL^b$. Regression equations were fitted to the log-transformed values of the variables, $\ln M = \ln a + b \times \ln SL$, in samples of *Desmognathus monticola* and *D. quadramaculatus* from the Wolf Creek (WC) and Coweeta Creek (Cow) watersheds.

Species	Sample	n	SL range	Parameters		R ²	95% CL of b
				a	b		
<i>D. monticola</i>	WC 1989 ¹	46	15.2–73.7	3.618×10^{-5}	2.853	0.993	2.782, 2.925
<i>D. monticola</i>	Cow 2007–2008 ²	46	17–65	5.573×10^{-5}	2.767	0.940	2.564, 2.971
<i>D. quadramaculatus</i>	Cow 2008–2009 ²	105	19–74	2.656×10^{-5}	2.981	0.926	2.817, 3.145
<i>D. monticola</i>	Cow 2009 ¹	30	11.9–73.8	2.433×10^{-5}	2.948	0.994	2.858, 3.038
<i>D. quadramaculatus</i>	Cow 2009 ¹	33	17.9–92.0	3.303×10^{-5}	2.899	0.994	2.813, 2.984

¹ Samples taken by the author.

² Data provided by John Maerz.

larvae in the sample. In the ANCOVA conducted on Coweeta *D. monticola* versus *D. quadramaculatus*, and limited to individuals ≤ 5 yr, the difference in slope was nonsignificant ($F = 0.690$; $df = 1, 127$; $P = 0.408$); the difference between species in standard length at a given age was significant ($F = 25.6$; $df = 1, 128$; $P < 0.001$). The ANCOVA of Coweeta versus Wolf Creek *D. monticola* also generated a nonsignificant difference in slope ($F = 2.29$; $df = 1, 123$; $P = 0.133$), but a significant difference in standard length at a given age ($F = 6.78$; $df = 1, 124$; $P = 0.010$).

For Coweeta *D. monticola* and *D. quadramaculatus*, the mean standard lengths of five-yr-old juveniles estimated from the regression equations were 54.0 and 55.5 mm, respectively. Given the small, nonsignificant difference in the regression coefficients and the relatively small difference in hatching sizes, I interpret the much greater sizes of adult males and females of *D. quadramaculatus* versus *D. monticola* as effects primarily of greater ages at first reproduction in the former species (Table 1).

As noted above, the Gompertz parameters differed significantly between Coweeta and Wolf Creek populations of *D. monticola*. Although the ANCOVA of juvenile standard length on age yielded a nonsignificant difference, the regression coefficient was higher for the Coweeta population. Application of the regression equations generated a difference in standard length of 3.8 mm at the approximate age (5 years) of first reproduction (Wolf Creek 50.2 mm, Coweeta 54.0 mm).

In fitting power functions to the data on body mass and standard length, I first log-transformed both variables, and fitted linear regression equations to the plots of \ln mass on \ln standard length. For *D. quadramaculatus*, ANCOVA detected no significant difference between the regressions of larvae and juveniles/adults, and the final regression was based on the pooled data. For *D. monticola*, the Wolf Creek sample included three larvae only, clustered at the lower end of the size distribution, and the Coweeta sample had a single tiny larva; in both cases the regressions included larvae and juveniles/adults. The Maerz sample of *D. monticola* included juveniles and adults only. The power functions of mass on standard length showed little variation between populations or between species, and in each the variance around the regression line was small (Table 3). Thus, the use of these equations for calculating estimated masses of the specimens in the 1994–1995 skeletochronological samples presumably introduced minimal errors. Subsequently, I fitted the derived Gompertz equations to the plots of mass on age (Fig. 3). In fitting the equations (Table 4), I used the a and b parameters from the autumn 2009 samples of *D. quadramaculatus* and *D. monticola* from Coweeta and the 1989 sample of *D. monticola* from Wolf Creek. These samples included wider ranges of body sizes of each species, and the regression analyses generated narrower confidence intervals of the regression coefficients than the Maerz data sets. The latter included fewer large adults, yet were useful for comparison; they generated similar pa-

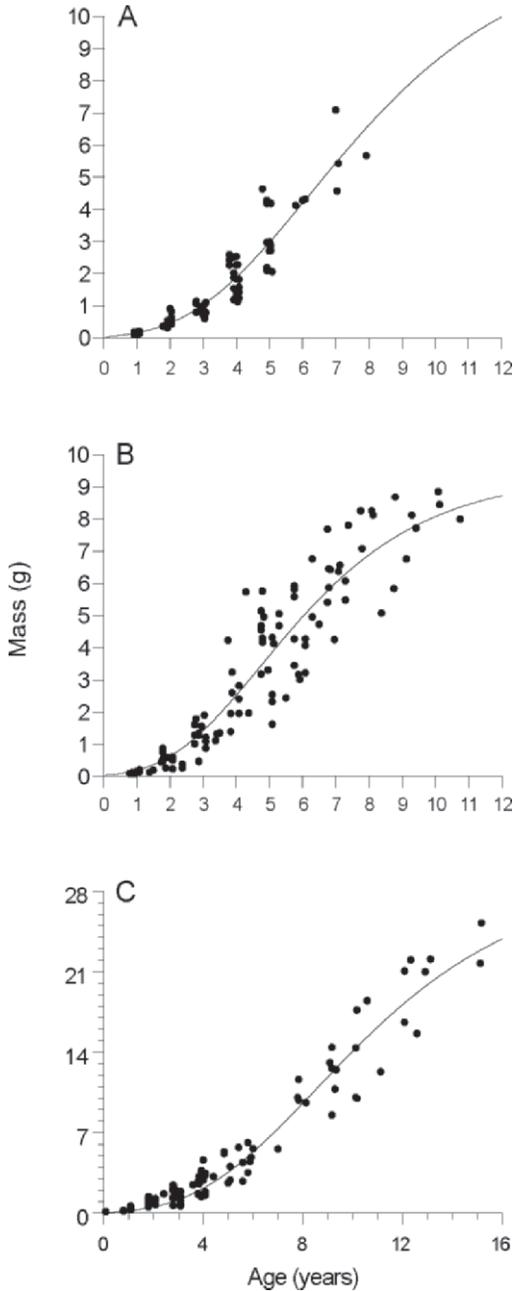


FIG. 3.—Plots of estimated mass against age for (A) Wolf Creek *Desmognathus monticola*, (B) Coweeta *D. monticola*, and (C) Coweeta *D. quadramaculatus*, fitted by the Gompertz function. As in Fig. 1, the fitted curves for *D. monticola* are extended beyond the range of the data, to 12 yr.

rameters, and confirmed the analysis of the mass–length relationship based on the other samples. Under the Gompertz model, the estimated ages of maximum rate of increase in mass were 8.5 yr for Coweeta *D. quadramaculatus* and 4.8 yr for Coweeta *D. monticola*; for each species these values lie within the combined male and female age range at first reproduction. For Wolf Creek *D. monticola*, the somewhat higher value of 6.7 yr, which is near the upper limit of female age at first reproduction, may be an effect of the small number of larger adults in this sample.

DISCUSSION

One source of error in using vertical or time-specific data to model individual growth is that the form of the graph may be affected by environmentally induced differences in the growth of individuals of different cohorts during comparable years of their lives (e.g., a two-yr-old individual might have had a different rate of growth in the first year of its life than a one-yr-old), solely on the basis of environmental differences between years. In relatively stable environments, like those experienced by *Desmognathus* salamanders in forested watersheds of the southern Blue Ridge Mountains, such effects are expected to be small.

In comparing life-history traits of species, restricting the evaluation to populations coexisting in a specific ecological community reduces the effects of such extrinsic factors as climate, resources, predators, and competitors, which can be assumed to be similar for the two species under consideration. The assumption is invalidated, in part, by niche differentiation between the species. In the present study, for the two Coweeta species, the null hypothesis of equivalent growth rates requires the assumption that the graphs of body size versus age represent patterns of intrinsic growth under the shared climatological and resource regimes of the Coweeta Creek ecosystem. Any differences in growth effected by differences in environmental conditions were minimized, given that the samples of both species were taken concurrently in and along the same streams. However, interactions between the species at Coweeta apparently involve both

TABLE 4.—Relationships fitted by the derived Gompertz growth function, $M_A = \{a^{1/b} \times SL_0 \exp[(\beta/\alpha)(1 - \exp)^{-\alpha \times A}]\}^b$, between body mass (M in g) and age (A in years) in two species of *Desmognathus* from the Coweeta Creek (Cow) and Wolf Creek (WC) watersheds. The 95% confidence limits are given in parentheses for the Gompertz parameters β and α .

Species	Parameters					R^2	M_0	M_{max}
	SL_0	a	b	β	α			
<i>D. monticola</i> (WC)	11.8	3.618×10^{-5}	2.853	0.556 (0.514, 0.598)	0.279 (0.245, 0.314)	0.875	0.041	12.18
<i>D. monticola</i> (Cow)	11.8	2.433×10^{-5}	2.948	0.686 (0.638, 0.734)	0.362 (0.330, 0.394)	0.880	0.035	9.38
<i>D. quadramaculatus</i> (Cow)	14.0	3.303×10^{-5}	2.899	0.440 (0.416, 0.464)	0.211 (0.196, 0.226)	0.948	0.069	29.30

competition and predation (Hairston, 1986, 1996), which might contribute to differential growth rates between the species. Nevertheless, it appears that growth rates of the two species are essentially identical through the larval and juvenile phases.

In a comparison of life history of *D. monticola*, Bruce and Hairston (1990) reported larger adult sizes at Coweeta versus Wolf Creek. They concluded that larval/juvenile growth rates were similar in the two populations, and that the differences stemmed from greater ages at first reproduction of both sexes at Coweeta. The skeletochronological analysis of Bruce et al. (2002) demonstrated overlap between populations in the age ranges at first reproduction of both males and females, but showed that there were higher proportions of both males and females maturing at younger ages at Wolf Creek than at Coweeta. In the present study, the slope of the regression of standard length on age of immatures was higher for Coweeta versus Wolf Creek, although the difference was not significant. Thus, larger adult sizes at Coweeta over Wolf Creek derive mainly from the slightly greater ages at first reproduction and, possibly, slightly higher larval and juvenile growth rates in the former population. It is likely that any difference in propagule size between these populations is negligible, and contributes minimally to the disparity in adult size. Differences in life history between Coweeta and Wolf Creek *D. monticola* may reflect genetic divergence, but may also be a direct effect of climatological differences between sites (Bruce et al., 2002).

The Gompertz plots of standard length on age show the slowing of growth with attain-

ment of sexual maturation in *Desmognathus*, as in other plethodontids (Marvin, 2001; Tilley, 1980). Point scatters around the curves reflect variation in growth. In all three populations the maximum rate of increase of standard length with age occurred at or nearly midway through the immature phase of the life cycle. However, increase in mass followed a different pattern, with the maximum rate occurring at or near the age at first reproduction. The difference is strictly a mathematical effect of the difference in the equations for length and mass, yet an association of sexual maturation with a damping of growth in body mass is biologically realistic.

In the two species of *Desmognathus* considered herein, most of the difference in size at first reproduction stems from differences in age at first reproduction, with the residual representing the difference in propagule size. Larval/juvenile growth rates are essentially equivalent. Such a trend is also evident for three smaller species of the genus, *D. ocoee*, *D. aeneus*, and *D. wrighti* (Bruce, 2009; Hining and Bruce, 2005). However, juvenile growth rates, at least at ages ≤ 3 yr, appear to be less in these earlier maturing species than in *D. monticola* and *D. quadramaculatus*.

Obviously, and in addition to genetic divergence, variation in any number of environmental factors may contribute to spatial and temporal variation in growth within species of *Desmognathus* (Bernardo and Agosta, 2003; Camp et al., 2000). However, based on the results of the present and earlier studies (Bruce, 1990, 2009), I suggest that within a given ensemble of *Desmognathus*, interspecific variation in body size is mainly an effect of differences in age at first reproduction, with

lesser contributions from variation in either propagule size or growth rate.

Adaptive radiation in *Desmognathus* has involved strong correlational selection on age and size at first reproduction especially. The larger species are older at first reproduction, and produce larger egg clutches that yield larger hatchlings (Tilley and Bernardo, 1993; Bruce, 1996, 2005). This suggests that selection for larger or smaller body size has involved a complex tradeoff in females involving age at first reproduction, clutch size, and propagule size, which serves to optimize age and size at first reproduction in terms of the distribution of mortality across larval, juvenile, and adult phases of the life cycle (Roff, 2002). Given that adult body size in *Desmognathus* is correlated with other morphological traits that reflect the adaptive zone of a species along the aquatic-to-terrestrial habitat gradient, this correlation raises the question of which environmental variables have contributed to the diversification in body size. Tilley (1968), Hairston (1986, 1996), and Kozak et al. (2005) emphasized the roles of predation and competition, whereas Bruce (1996) focused on qualitative and quantitative variation in such cover objects as rocks, logs, moss, and leaf litter. Although the relative importance of intraguild predation in structuring *Desmognathus* ensembles is unresolved (Camp, 1997), a wealth of experimental evidence (reviewed in Bruce, 2007, 2008; Wells, 2007) suggests that interspecific interactions, in combination with opportunities for resource exploitation along the aquatic-to-terrestrial habitat gradient in mesic forest environments of eastern North America, have promoted the observed variation in body size and correlated life-history traits in this remarkable genus.

Acknowledgments.—I thank J. Castanet and H. Francillon-Vieillot, my colleagues in the earlier study upon which this study is derived. J. Maerz graciously provided unpublished data on Coweeta *Desmognathus*. J. Bruce assisted with the graphics. My field work was supported by Western Carolina University and Highlands Biological Station. Specimens were treated in accordance with Animal Care and Use guidelines of Western Carolina University and Highlands Biological Station. Collecting permits were issued by the North Carolina Wildlife Resources Commission and the Coweeta Hydrologic Laboratory, Nantahala National Forest.

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Accepted: 12 August 2010
Associate Editor: Michael Freake

APPENDIX I

(1) The Gompertz function: $SL_A = SL_0 \exp\{[\beta/\alpha][1 - \exp(-\alpha \times A)]\}$.

The first and second derivatives of the Gompertz equation are

$$\begin{aligned} dSL/dA &= \beta \times SL_0 \exp\{[\beta/\alpha][1 - \exp(-\alpha \times A)] - \alpha \times A\}, \\ \text{and} \\ d^2SL/dA^2 &= \beta^2 \times SL_0 \times \\ &\exp\{[\beta/\alpha][1 - \exp(-\alpha \times A)] - 2\alpha \times A\} - \beta \times \alpha \times SL_0 \times \\ &\exp\{[\beta/\alpha][1 - \exp(-\alpha \times A)] - \alpha \times A\}. \end{aligned}$$

Setting $d^2SL/dA^2 = 0$, and solving for A gives the age at the rate of maximum growth, $A_\lambda = \ln(\beta/\alpha)/\alpha$. Substituting this value into (i) the Gompertz equation and (ii) the first derivative gives (i) the size at this age and (ii) the maximum value of the growth rate.

(2) The Gompertz function for growth in mass: $M_A = \{a^{1/b} \times SL_0 \exp[(\beta/\alpha)(1 - \exp(-\alpha \times A))] \}^b$.

The first derivative is

$$\begin{aligned} dM/dA &= a^{1/b} \times SL_0 \times b \times \\ &\beta \{ a^{1/b} \times SL_0 \exp[(\beta/\alpha)(1 - \exp(-\alpha \times A))] \}^{b-1} \times \\ &\exp\{[\beta/\alpha][1 - \exp(-\alpha \times A)] - \alpha \times A\}. \end{aligned}$$

Let $u = a^{1/b} \times SL_0 \times b \times \beta \{ a^{1/b} \times SL_0 \exp[(\beta/\alpha)(1 - \exp(-\alpha \times A))] \}^{b-1}$ and $v = \exp\{[\beta/\alpha][1 - \exp(-\alpha \times A)] - \alpha \times A\}$.

For the second derivative calculate $u(dv/dA) + v(du/dA)$.

$$\begin{aligned} d^2M/dA^2 &= \left\{ a^{1/b} \times SL_0 \times b \times \right. \\ &\beta \left[a^{1/b} \times SL_0 \exp\{(\beta/\alpha)[1 - \exp(-\alpha \times A)]\} \right]^{b-1} \\ &\times \exp[-\alpha \times A + (\beta/\alpha)(1 - \exp(-\alpha \times A))] \times \\ &[-\alpha + \beta \exp(-\alpha \times A)] + \\ &\left\{ \exp(-\alpha \times A + [\beta/\alpha][1 - \exp(-\alpha \times A)]) \right\}^2 \times \\ &\left[a^{2/b} \times SL_0^2 \times \beta^2 \times b \times (b-1) \right] \times \\ &\left. \left[a^{1/b} \times SL_0 \exp\{(\beta/\alpha)[1 - \exp(-\alpha \times A)]\} \right]^{b-2} \right\} \end{aligned}$$

Set $d^2M/dA^2 = 0$, and let $u(dv/dA) = -v(du/dA)$. Simplify and solve for A; thus, $A_\lambda = \ln[(b \times \beta)/\alpha]/\alpha$, the age at the maximum rate of growth in mass. As in (1), substituting this value into (i) the Gompertz equation for growth in mass, and (ii) the first derivative gives (i) the size at this age and (ii) the maximum value of the growth rate.