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Application of the Gompertz Function in Studies of Growth in Dusky Salamanders (Plethodontidae: *Desmognathus*)

Richard C. Bruce¹

Gompertz growth functions were fitted to skeletochronological data sets of three species of desmognathine salamanders from an assemblage (Wolf Creek) in the Cowee Mountains of southwestern North Carolina. The results were compared to earlier evaluations of growth in desmognathines from a nearby assemblage (Coweeta) in the Nantahala Mountains. In two of the species, *Desmognathus quadramaculatus* and *D. monticola*, larger adult body sizes were attained at Coweeta than at Wolf Creek, whereas adult body sizes of the third species, *D. ocoee*, were similar in the two populations. Growth in both standard length (snout–vent length) and body mass were evaluated. The early phases of growth, prior to sexual maturation, were similar in the larger *D. quadramaculatus* and the smaller *D. monticola*, and higher in both species than in the even smaller *D. ocoee*. In all three species, growth rates tended to be higher in the Coweeta populations than in those at Wolf Creek. The inflexions of the Gompertz curves for body mass versus age, representing the maximum rates of growth, occurred at or near the age of first reproduction, which is expected, given the tendency for growth to slow at sexual maturation in desmognathines and other salamanders. The results support earlier findings that differences in adult body size between *D. quadramaculatus* and *D. monticola* are mainly effects of differences in age at sexual maturation, modulated by a difference in propagule size, as opposed to growth differences. However, the difference in adult size between these species and *D. ocoee* are joint effects of smaller propagule size, lower growth rate, and earlier maturation in the latter species.

IN the southern Blue Ridge Physiographic Province, assemblages of desmognathine salamanders in small watersheds usually contain three to six species (Bruce, 2011). Three core members of such assemblages, listed in order of decreasing body size, are *Desmognathus quadramaculatus*, *D. monticola*, and a member of the *D. ochrophaeus* complex (*D. orestes*, *D. carolinensis*, or *D. ocoee*). These species demonstrate the trend in *Desmognathus* that larger species are more aquatic and smaller forms more terrestrial (e.g., Hairston, 1949:fig. 10; Organ, 1961:fig. 2; Hairston, 1980:table 2; Petranka and Smith, 2005:fig. 3). In assemblages having additional species, the relationship between body size and habitat use is generally maintained (Bruce, 2011). Proximate factors contributing to body-size differences among species of *Desmognathus* include propagule size, growth rate, and age at sexual maturation. To further clarify the effects of these factors, in this study I examine variation in growth in an assemblage of desmognathines comprising the core species *D. quadramaculatus*, *D. monticola*, and *D. ocoee*, and compare the results to those of an earlier study of a nearby assemblage (Bruce, 2010).

Empirical studies of growth in salamanders have often employed mark–recapture methods (Tilley, 1980; Staub et al., 1995; Marvin, 2001; Lee et al., 2012) or skeletochronology (Miaud et al., 2000; Miaud and Guillaume, 2005; Üzümlü and Olgun, 2009). A general pattern observed in salamanders involves a phase of rapid early growth, a marked slowing of growth at the age of sexual maturation, and a further reduction at older ages. Several investigators have fitted von Bertalanffy growth functions to either mark–recapture or skeletochronological data (Miaud and Guillaume, 2005; Üzümlü and Olgun, 2009; Lee et al., 2012). Marvin (2001), however, fitted Gompertz growth equations to mark–recapture data of *Plethodon kentucki*. Although growth models have been developed in recent years that purportedly perform better than the von Bertalanffy and Gompertz (e.g., Hernandez-Llamas and Ratkowsky, 2004; Bhowmick and Bhattachar-

ya, 2014), I know of no application of these models in studies of salamander growth.

In a landmark study of growth in *Desmognathus*, Tilley (1980) conducted a mark–recapture study in two populations of *D. ocoee* during seven growing seasons. His growth curves showed the general pattern of rapid early growth, a slow-down at sexual maturation, and a flattening of the growth curve at older ages, with slower growth in females than males. He reported that higher-elevation salamanders grew at slower rates than those at a lower-elevation site and attained smaller adult sizes.

In earlier papers (Bruce, 2009, 2010), I fitted Gompertz and von Bertalanffy growth functions to skeletochronological age data for several populations of desmognathine salamanders. The analyses of the relationship between body size and age were based on samples of three species from two assemblages (Wolf Creek, Coweeta Creek) in the southern Blue Ridge of southwestern North Carolina, as reported in Bruce et al. (2002). The objective was to generate growth curves as part of an evaluation of factors contributing to variation in adult body size among species of *Desmognathus*. I concluded that age at first reproduction and propagule size (egg and hatching size) were the most important contributors to differences in adult body size among the species investigated. For *D. quadramaculatus* and *D. monticola*, in reference to growth rate as estimated by the Gompertz function, I suggested that the maximum rate of increase in standard (snout-to-vent) length occurred approximately midway through the immature (larva plus juvenile) phase of the life cycle, but that of body mass occurred at or near the age of first reproduction (Bruce, 2010). The Gompertz function was considered a more realistic model of growth than the von Bertalanffy function because it better estimated the sigmoidal pattern of early growth, in contrast to the exponential form of the von Bertalanffy function. For one species, *D. ocoee*, I fitted a Gompertz function to just the length data and thus evaluated growth in length only (Bruce, 2009).

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At the time these studies were conducted, three skeletochronological data sets from an earlier study of Wolf Creek desmognathines (Castanet et al., 1996) were missing and were thought to be irretrievably lost. However, these data have since been recovered, and form the basis of the present report. Thus, the objectives of the present study are (1) to evaluate growth in standard length and body mass in populations of *D. quadramaculatus* and *D. ocoee* in the Wolf Creek assemblage; (2) to reexamine growth in *D. monticola* at Wolf Creek vis-à-vis the analysis of the sample evaluated in Bruce (2010), which was deficient in adults; (3) to extend the analysis of the Coweeta Creek population of *D. ocoee* reported in Bruce (2009), in order to include an evaluation of growth in mass; and (4) to compare the results with those of the populations of Coweeta Creek *D. quadramaculatus* and *D. monticola* evaluated earlier (Bruce, 2010). For comparison with the Coweeta findings, I have evaluated the Wolf Creek data with the Gompertz growth model only. The Wolf Creek data set provides a means of (1) evaluating the contribution of growth rate differentials to variation in adult body size among the species in these assemblages, and (2) testing the hypothesis that maximal rates of growth in mass occur at or near the age of sexual maturation in *Desmognathus*.

MATERIALS AND METHODS

The analyses of growth are based on skeletochronological data sets of three species, as described in Castanet et al. (1996). I have also extended the analysis (Bruce, 2009) of the Coweeta Creek data set of *D. ocoee* described in Bruce et al. (2002). Locality data for the Wolf Creek site in the Cowee Mountains of Jackson County, North Carolina, and the Coweeta Creek site in the Nantahala Mountains of Macon County, North Carolina, are given in Castanet et al. (1996) and Bruce et al. (2002), respectively. Sampling and histological methods are described in those papers. Whereas age (*A*) in those studies was estimated to the nearest year, I have recalculated ages in years to the nearest half month, based on sampling dates and estimated median hatching dates for each species: *D. quadramaculatus*, 1 August; *D. monticola*, 15 August; *D. ocoee*, 1 September. These dates are based on findings presented in Bruce (1990), Bruce (2009), and Bruce (2014), as well as on unpublished observations of nesting females and egg clutches in various stages of development at both localities over many years. Hatching dates for each of the three species are similar at Wolf Creek and Coweeta Creek. Hatching sizes (SL_0) are based on results in Bruce (1990) and unpublished data. For measurements of body mass of *D. ocoee*, I pooled samples from Coweeta with those from sites in the adjacent Nantahala River watershed described in Bruce (2009).

The skeletochronological data from Wolf Creek included 100 *D. quadramaculatus*, 83 *D. monticola*, and 76 *D. ocoee* in which well-expressed annual lines of arrested growth (LAGs) could be counted (Castanet et al., 1996). For Coweeta Creek *D. ocoee*, 101 individuals were reliably aged by skeletochronology (Bruce et al., 2002). Specimens rejected because of difficulty in counting LAGs included 1 *D. quadramaculatus*, 7 *D. monticola*, and 11 *D. ocoee* from Wolf Creek, and 5 *D. ocoee* from Coweeta.

Inasmuch as the salamanders aged by skeletochronology were not weighed, for each such individual I estimated its body mass from regressions of log-transformed values of body mass (*M*) on standard length (*SL*) in samples of 53 *D. quadramaculatus*, 56 *D. monticola*, and 57 *D. ocoee* from Wolf

Creek, and 113 *D. ocoee* from the Coweeta/Nantahala River sites. The salamanders were anesthetized in MS-222, lightly blotted with paper toweling, weighed to the nearest 0.001 g, and measured from tip of snout to caudal edge of vent to the nearest 0.1 mm. They were then rinsed in spring water, revived, and released near the capture location. The size measurements were log-transformed, and regressions of $\ln M$ on $\ln SL$ ($\ln M = \ln a + b \cdot \ln SL$) were fitted to the data. Differences among regressions were evaluated with ANCOVA.

In fitting Gompertz functions to the *SL* vs. age and mass vs. age data, I used the equations given in Bruce (2010), namely $SL_A = SL_0 \cdot \exp[(\beta/\alpha)(1 - \exp(-\alpha \cdot A))]$, and $M_A = [a^{(1/b)} \cdot SL_0 \cdot \exp[(\beta/\alpha)(1 - \exp(-\alpha \cdot A))]]^b$. β and α are the Gompertz parameters, where β = the initial specific growth rate of either *SL* or *M*, and α = the rate of decay of β . For both functions, I took first and second derivatives, and calculated estimates of the age and size of maximum growth and the maximum growth rate, using the derivations given in Bruce (2010). I was not able to separately analyze males and females because larvae and small immatures were not sexed and because sample sizes of adults were relatively small.

Mathematical and statistical procedures were done with Mathematica7 (Wolfram Research) and SYSTAT v.10.2 and SYSTAT 12 (Systat Software, Inc.).

RESULTS

The Gompertz functions provided reasonably good approximations of the trends shown by the scatterplots of *SL* versus age (Fig. 1). The goodness of fit of the data to the Gompertz equations (Table 1) were stronger for the two larger species ($R^2 \geq 0.95$) than for *D. ocoee* ($R^2 = 0.829$), as indicated by the greater point scatter around the curve of *D. ocoee* versus the other two species. Maximum *SL*s in the skeletochronological samples were nearly equivalent to the estimated asymptotic *SL*s in both *D. quadramaculatus* (94.1 vs. 95.0 mm) and *D. monticola* (70.3 vs. 71.6 mm), but less in *D. ocoee* (48.4 vs. 52.7 mm). The Gompertz application suggested that growth rates of larval and immature *D. quadramaculatus* and *D. monticola* were nearly identical, and higher than in *D. ocoee* (Fig. 2A).

In comparing these results with an extended analysis of those of the previous studies (Bruce, 2009, 2010), I suggest, first, that the 1989–93 data for Wolf Creek *D. monticola*, presented herein, are more reliable than the later (1995) data given in Bruce (2010) because of the smaller number of larger, older adults in the 1995 sample. Thus, in discounting the latter sample in the comparisons of species/populations, it appears that ages and standard lengths at the maximum rates of growth are greater in each species at Coweeta than at Wolf Creek, and in both assemblages such maxima occur in the larval/juvenile phases of the life cycle (Table 2). However, in both assemblages, the maximum values of the growth rate in standard length, at A_x , are similar in *D. quadramaculatus* and *D. monticola*, and higher in both species than in *D. ocoee*.

In the regressions of $\ln M$ on $\ln SL$, the close fit of the $\ln M$ values to the regression lines ($R^2 \geq 0.98$) justified the assignment of body masses to the salamanders aged by skeletochronology from the regression equations (Table 3). Errors introduced into the body mass–age relationships by this procedure were considered minimal. In each case the regression coefficients were slightly less than the predicted value of 3.0 for a regression of mass on a linear dimension. Although the slopes of the $\ln M$ – $\ln SL$ regressions of the three Wolf Creek species were similar, and the regression lines

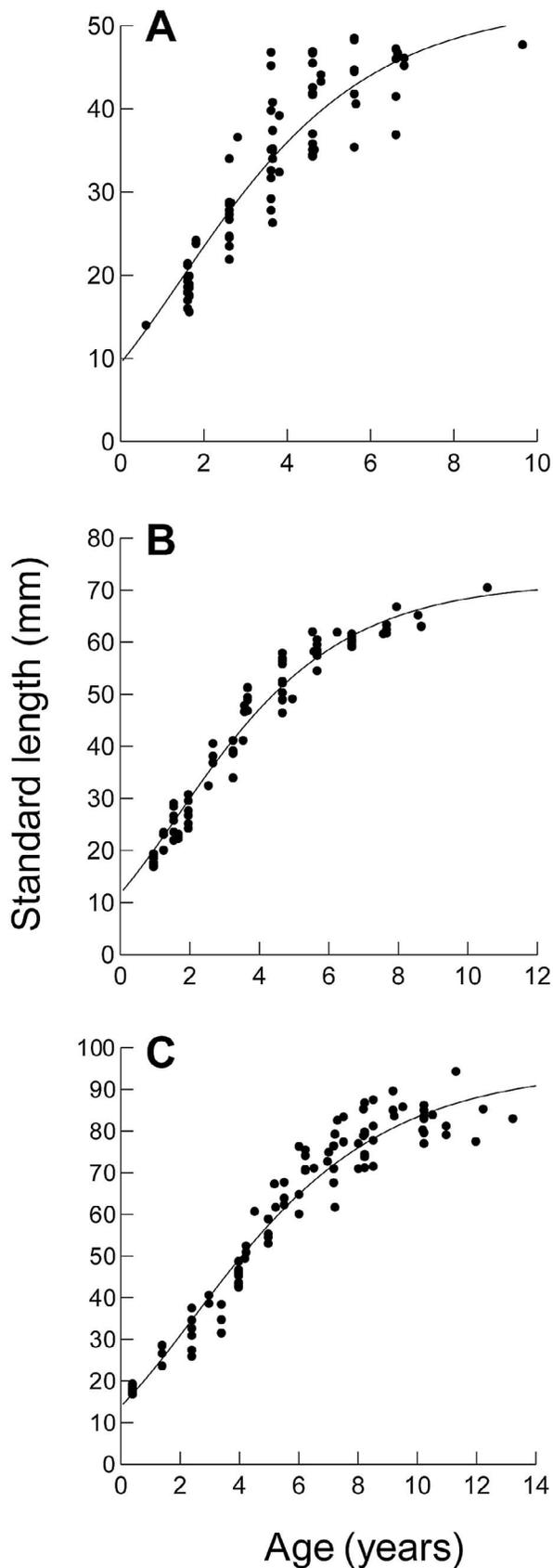


Fig. 1. Gompertz curves fitted to plots of standard length against age for Wolf Creek (A) *Desmognathus ocoee*, (B) *D. monticola*, and (C) *D. quadramaculatus*. Curves are derived from the equations in Table 1. Note the slight sigmoidal form of the curves. Intercepts are equal to the mean hatching sizes (SL_0) of the three species. The upper asymptotes (SL_{max}) are close to the maximum SLs observed in these populations (see text).

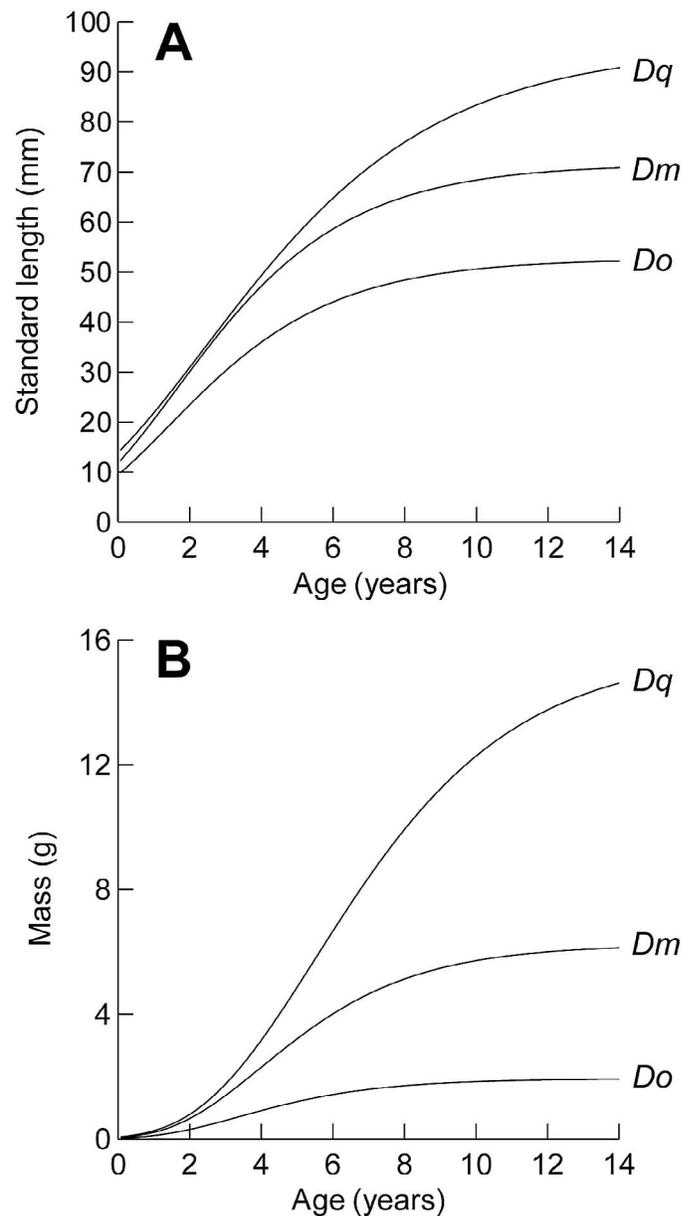


Fig. 2. Gompertz curves from (A) Figure 1 and (B) Figure 3 drawn to the same scale for the three Wolf Creek species of *Desmognathus*. The greater similarity of the early phases of growth of *D. quadramaculatus* and *D. monticola* versus that of *D. ocoee* is evident, especially for growth in SL.

nearly coincident, ANCOVA applied to the regressions yielded a significant interaction between species and $\ln SL$ ($F_{2,160} = 7.757$, $P = 0.001$), precluding a test for a difference in $\ln M$. Evaluation of the $\ln M$ - $\ln SL$ regressions of the Wolf Creek and Coweeta/Nantahala samples of *D. ocoee* yielded a marginally significant interaction between population and $\ln SL$ ($F_{1,166} = 4.879$, $P = 0.029$).

The Gompertz equations fitted to the body mass and age estimates (Table 4) showed, as expected, wider point scatters around the fitted growth curves (Figs. 3, 4), as well as poorer fits of the curves to the data and lower R^2 values than the Gompertz equations of SL on age, especially for *D. quadramaculatus* and *D. ocoee*. In evaluating rate maxima (Table 5), I again considered the 1989–93 sample of Wolf Creek *D. monticola* more reliable than the 1995 sample. For all three species the age at the estimated maximum rate of increase in

Table 1. Relationships fitted by the Gompertz function between standard length (SL in mm) and age (A in years) in populations of *Desmognathus* at Wolf Creek, where $SL_A = SL_0 \cdot \exp[(\beta/\alpha) \cdot (1 - \exp(-\alpha A))]$. The 95% confidence limits are given in parentheses for the Gompertz parameters β and α , where β = initial specific growth rate in SL and α = rate of decay of β .

Species	SL ₀ (mm)	Gompertz parameters		SL _{max} (mm)	R ²
		β	α		
<i>D. quadramaculatus</i>	13.9	0.517 (0.486, 0.548)	0.269 (0.246, 0.291)	95.0	0.952
<i>D. monticola</i>	11.8	0.660 (0.625, 0.696)	0.366 (0.339, 0.394)	71.6	0.964
<i>D. ocoee</i>	9.44	0.648 (0.578, 0.717)	0.377 (0.316, 0.438)	52.7	0.829

Table 2. Rate maxima for standard length (SL) based on Gompertz parameters of Table 1 and those in Bruce (2009, 2010). The values were calculated based on equations in Bruce (2010:appendix I).

Species (population)	Age (yr) at maximum rate of growth in SL, $A_\lambda = (\ln(\beta/\alpha))/\alpha$	SL _{Aλ} (mm)	Maximum value of the growth rate (mm/yr), dSL/dA_λ
<i>D. quadramaculatus</i> (WC) ^a	2.43	34.94	9.40
<i>D. monticola</i> (WC) ^a	1.61	26.35	9.64
<i>D. monticola</i> (WC) ^b	2.73	33.34	8.70
<i>D. ocoee</i> (WC) ^a	1.44	19.37	7.30
<i>D. quadramaculatus</i> (Cow) ^b	2.88	38.55	9.36
<i>D. monticola</i> (Cow) ^b	1.97	29.83	9.94
<i>D. ocoee</i> (Cow) ^c	1.51	20.44	7.91

^a From Table 1 of this paper, 1989–1993 samples

^b Calculated from results in Bruce (2010), 1994–1995 samples

^c Calculated from results in Bruce (2009), 1994–1995 samples

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

Species	Sample	n	Parameters		R ²
			a	b	
<i>D. quadramaculatus</i>	WC	53	2.203×10^{-5}	2.994	0.989
<i>D. monticola</i>	WC	56	2.974×10^{-5}	2.898	0.990
<i>D. ocoee</i>	WC	57	4.039×10^{-5}	2.767	0.988
<i>D. ocoee</i>	Cow	113	2.462×10^{-5}	2.890	0.981

Table 4. Relationships fitted by the Gompertz function between body mass (M in g) and age (A in years) in populations of *Desmognathus* at Wolf Creek (WC) and Coweeta (Cow), where $M_A = \{a^{1/b} \cdot SL_0 \cdot \exp[(\beta/\alpha) \cdot (1 - \exp(-\alpha A))]\}^b$. The 95% confidence limits are given in parentheses for the Gompertz parameters β and α , where β = initial specific growth rate in M and α = rate of decay of β . The values of the regression parameters a and b are from Table 3.

Species (population)	SL ₀	Parameters				R ²	M ₀	M _{max}
		a	b	β	α			
<i>D. quadramaculatus</i> (WC)	13.9	2.203×10^{-5}	2.994	0.585 (0.541, 0.628)	0.313 (0.285, 0.342)	0.895	0.058	15.68
<i>D. monticola</i> (WC)	11.8	2.974×10^{-5}	2.898	0.718 (0.680, 0.756)	0.408 (0.381, 0.435)	0.953	0.038	6.23
<i>D. ocoee</i> (WC)	9.44	4.039×10^{-5}	2.767	0.742 (0.648, 0.836)	0.450 (0.375, 0.524)	0.749	0.020	1.93
<i>D. ocoee</i> (Cow)	9.24	2.462×10^{-5}	2.890	0.766 (0.696, 0.835)	0.442 (0.387, 0.497)	0.843	0.015	2.28

mass occurred near the ages of sexual maturation, i.e., just below the earliest age at maturation or within the combined range of age at first reproduction of males and females (see Castanet et al., 1996; Bruce et al., 2002). Within species, the maximal values of the growth rate in mass were higher at Coweeta than at Wolf Creek, and, among species, the larger species had higher maximal growth rates. As in the plots of SL versus age, the Gompertz curves of mass versus age for the Wolf Creek populations suggested that early growth in body

mass is very similar in *D. quadramaculatus* and *D. monticola*, and higher in both species than in *D. ocoee* (Fig. 2B).

DISCUSSION

Earlier studies have shown that in *D. quadramaculatus* and *D. monticola*, larger body sizes are attained at Coweeta than at Wolf Creek, and that these differences are correlated with larger sizes and greater ages at sexual maturation (Bruce and Hairston, 1990; Castanet et al., 1996; Bruce et al., 2002).

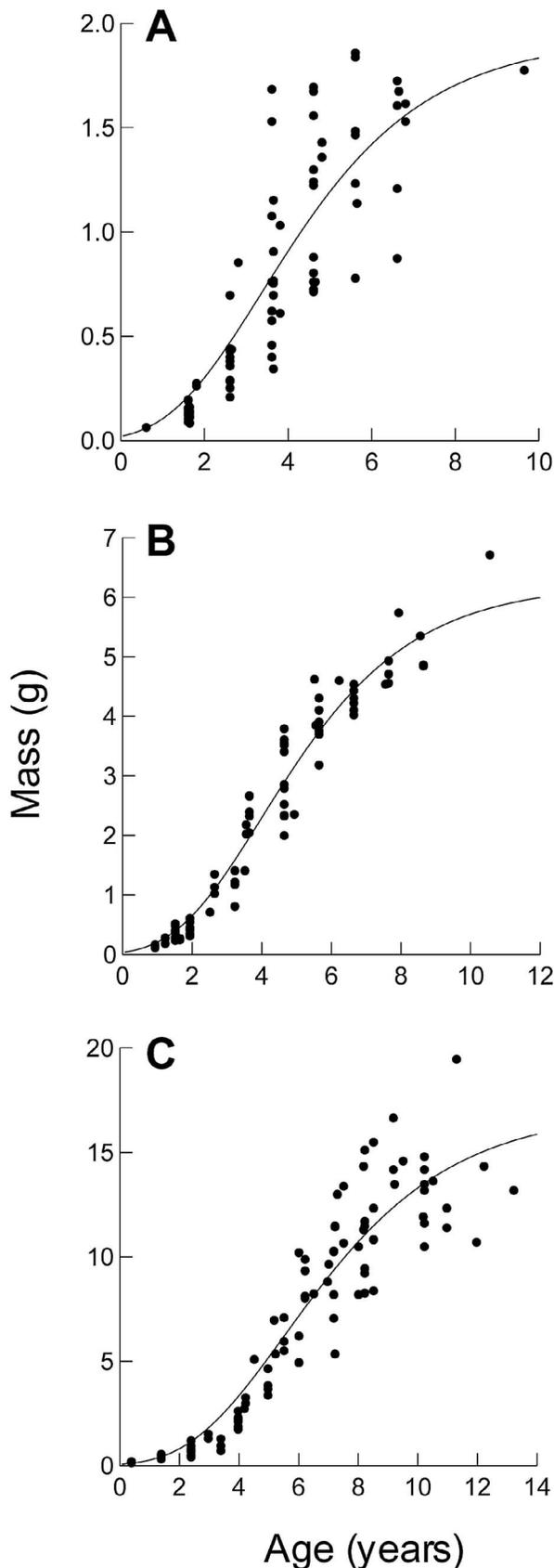


Fig. 3. Gompertz curves fitted to plots of estimated mass against age for Wolf Creek (A) *Desmognathus ocoee*, (B) *D. monticola*, and (C) *D. quadramaculatus*. Curves are derived from the equations in Table 4. The sigmoidal form of the curves is better expressed than in those of SL versus age, an effect of the relationship between standard length and mass, where $M = aSL^b$.

However, for *D. ocoee* no apparent differences in body size or age at maturation were detected in the skeletochronological studies (Castanet et al., 1996; Bruce et al., 2002).

The similarities in the Gompertz curves of *D. quadramaculatus* and *D. monticola* during the early phases of life (especially growth in SL), and the presumptively slower early growth of *D. ocoee*, parallel the results for the Coweeta populations of these species (Bruce, 2009, 2010). The findings reinforce the contention that differences between *D. quadramaculatus* and *D. monticola* in age at first reproduction is the principal contributor to differences in size at first reproduction and adult size, with a secondary contribution from a difference in propagule size. In contrast, a lower rate of early growth serves to complement the role of early maturation and small propagule size in eliciting smaller body size in *D. ocoee* versus the two larger congeners.

For the other two species that occur both at Coweeta and in the adjacent Nantahala River watershed, i.e., *D. aeneus* and *D. wrighti*, life history comparisons with *D. ocoee* have been treated by methods other than skeletochronology (Bruce, 2009). A sixth species, *D. marmoratus*, intermediate in size between *D. quadramaculatus* and *D. monticola*, and found only at the Nantahala River sites, has not been studied.

In addition to the data sets treated herein, there are other body-size data for the Wolf Creek populations of *Desmognathus* (Bruce, 1988, 1990, 1995, and unpubl.). In these samples, maximum body lengths were similar to or slightly greater than those predicted by the asymptotes of the Gompertz curves: three individuals 72–74 mm SL among 3,517 *D. monticola* (asymptote 71.6 mm), one individual 52 mm SL among 1,210 *D. ocoee* (asymptote 52.7 mm), and three individuals 96–99 mm SL among 154 *D. quadramaculatus* (asymptote 95.0 mm).

For vertical or time-specific data such as the skeletochronological data sets evaluated herein, the scatters of points around the Gompertz curves reflect individual variation in growth, including annual variation in environmental effects on growth, as well as differences between sexes in adult growth rate (e.g., Tilley, 1980), but may also incorporate skeletochronological errors (Castanet et al., 1996). In addition, the point scatters in the plots of body mass against age incorporate relatively small errors originating from the derivative values of mass. Thus, the Gompertz equations derived from skeletochronological estimates represent a first approximation of the “average” growth pattern of an individual salamander. Assuming that potential methodological errors are small, the plots indicate high levels of variation in growth in all three species.

In the Wolf Creek samples, some of the variation among same-age individuals probably traces to the four-year interval over which the samples were taken. Such effects of year-of-capture have been found in other amphibians (e.g., Cogălniceanu et al., 2014). However, growth curves based on time-specific data will inevitably reflect environmentally induced differences in growth between members of different cohorts during comparable phases of their lives. For this reason, horizontal data on single individuals may provide a better picture of growth and its variation.

The documented differences in body size between Wolf Creek and Coweeta *D. quadramaculatus* and *D. monticola* are reflected in the differences between the derived growth parameters determined from the inflexions of the Gompertz curves; i.e., the greater values of age and body size at the maximum rates of growth in both standard length and body mass in the Coweeta vis-à-vis the Wolf Creek populations of

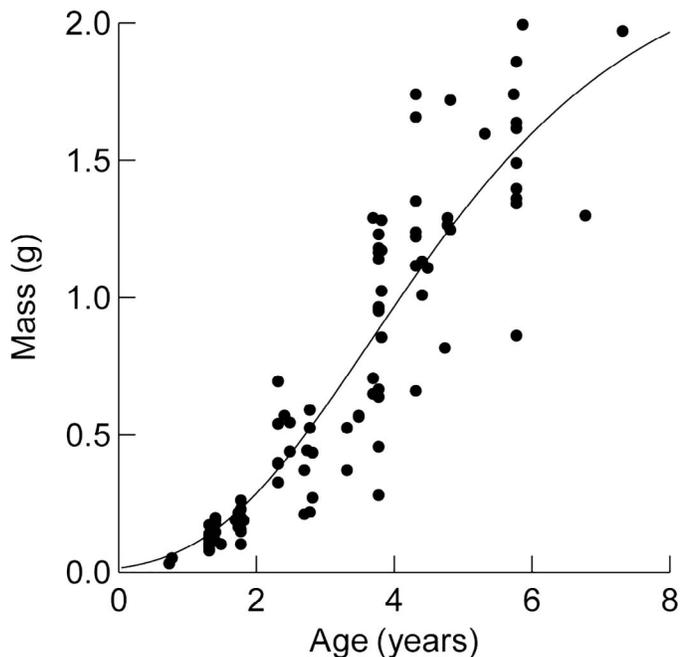


Fig. 4. Gompertz curve fitted to plot of estimated mass against age for Coweeta *Desmognathus ocoee*. Curve is derived from the equation in Table 4. Note similarity to graph A of Wolf Creek *D. ocoee* in Figure 3.

the two species. In contrast, body sizes are similar in Coweeta and Wolf Creek *D. ocoee*. Whereas the comparable growth parameters for *D. ocoee* are higher at Coweeta versus Wolf Creek, the differences are much less than in *D. quadramaculatus* and *D. monticola*.

In all three species in both assemblages the age at the maximum value of the growth rate in mass occurred just prior to maturation or within the range of male and female age at first reproduction, a finding previously reported for *D. monticola* and *D. quadramaculatus* (Bruce, 2010). This relationship probably applies to other desmognathines (Tilley, 1980) and plethodontids generally (e.g., Marvin, 2001; Lee et al., 2012), although these authors studied growth in SL rather than mass. D'Arcy Thompson (1942:157), in noting that the inflexion of the Gompertz curve is about one-third of the way between asymptotes (actually $\exp[-1]$), claimed that size at the inflexion has no biological significance relative to the growth of the individual. In the present application, the inflexion of the Gompertz equation for growth in mass

occurs close to the age at first reproduction, which appears biologically realistic in terms of shift of allocation of resources at reproduction. However, this relationship needs to be examined separately in each sex.

The maximum values of the growth rate in standard length of *D. quadramaculatus* and *D. monticola* were similar between species and between localities, whereas those of *D. ocoee* were similar at Coweeta and Wolf Creek but lower than those of the two larger species. In contrast, for the estimates of the maximum rate of growth in body mass, the values for *D. quadramaculatus* were higher than those of *D. monticola*, and higher in both species at Coweeta than at Wolf Creek. Again, the values for *D. ocoee* were lower than those of the other two species, but similar for the two populations.

The above comparisons apply only to the gross rate of size increase. Although a full analysis was not undertaken, relative growth rates, i.e., $(dSL_A/dA)/SL_A$ and $(dM_A/dA)/M_A$, are maximal at hatching and decline monotonically with age.

These three species of *Desmognathus* conform to the general pattern in the genus wherein larger species tend to be more aquatic and the smaller more terrestrial. At both Wolf Creek and Coweeta there is considerable overlap in habitat use, especially in and along smaller streams, where the assemblage is often a mélange of all three species. Presumably, body-size differentials in *Desmognathus* are products of natural selection on life-history traits, acting in concordance with adaptive diversification in morphology and modulated by the underlying genetic architecture (e.g., de Jong and van Noordwijk, 1992; Roff and Fairbairn, 2007). Selective factors ostensibly include climatological influences, habitat gradients, resource distributions, and species interactions in the diverse stream and forest ecosystems of the Appalachian Mountains. In *Desmognathus*, including the three species of this study, there are correlations among body size, growth, and age at first reproduction, as reported herein and elsewhere (Castanet et al., 1996; Bruce et al., 2002), and also involving fecundity, propagule size, and mortality (Tilley and Bernardo, 1993; Bruce, 2009, 2010, 2013, 2014). Essentially, the evolution of larger body size in the more aquatic species provides for higher fecundity and larger propagules, and perhaps better parental care, but requires longer generation times and results in lower survival to first reproduction than in the smaller, more terrestrial species. Such relationships suggest that life-history evolution in the genus has been mediated by synergistic trade-offs among growth, mortality, and reproductive allocation, as

Table 5. Rate maxima for body mass (M) based on Gompertz parameters of Table 4 and those in Bruce (2009, 2010). The values were calculated based on equations in Bruce (2010:appendix I).

Species (population)	Age (yr) at maximum rate of growth in mass, $A_\lambda = (\ln(b\beta/\alpha))/\alpha$	M_{A_λ}	Maximum value of the growth rate (g/yr), dM/dA_λ
<i>D. quadramaculatus</i> (WC) ^a	5.50	5.77	1.805
<i>D. monticola</i> (WC) ^a	3.99	2.29	0.938
<i>D. monticola</i> (WC) ^b	6.23 ^c	4.48	1.250
<i>D. ocoee</i> (WC) ^a	3.37	0.71	0.320
<i>D. quadramaculatus</i> (Cow) ^b	8.53	10.78	2.274
<i>D. monticola</i> (Cow) ^b	4.75	3.45	1.248
<i>D. ocoee</i> (Cow) ^d	3.65	0.84	0.370

^a From Table 4 of this paper, 1989–1993 samples

^b Calculated from results in Bruce (2010), 1994–1995 samples

^c A_λ corrected from the value given in Bruce (2010)

^d From Table 4 of this paper, representing the extended analysis of results in Bruce (2009), 1994–95 samples

documented in fish by Roff et al. (2006). Testing of these relationships in a greater variety of desmognathine assemblages would be helpful in extending our understanding of life-history evolution in the genus. In the evaluation of growth itself, long-term mark-recapture studies of the several species in one or more multispecies assemblages would complement results based on the time-specific, vertical method, as reported in the present study.

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