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Among salamanders of the genus *Desmognathus*, the larger species tend to be more aquatic and the smaller more terrestrial. I studied life histories in assemblages of *Desmognathus* in the southern Blue Ridge Mountains of North Carolina at sites in the Cowee and southern Nantahala Mountains. Traits evaluated included mortality/survival, age at first reproduction, fecundity, and body size. The first three are direct fitness traits that enter into the characteristic equation, ${}_{x=\alpha}\Sigma^{\infty} l_x m_x e^{-rx} = 1.0$. One assemblage (Wolf Creek), in the Cowee Mountains, comprises three species, from larger to smaller, *D. quadramaculatus*, *D. monticola*, and *D. ocoee*. A second assemblage (Coweeta Creek), in the Nantahala Mountains, also includes *D. quadramaculatus*, *D. monticola*, and *D. ocoee*, as well as the smaller *D. aeneus* and *D. wrighti*. I also studied three species only (*D. ocoee, D. aeneus, D. wrighti*) in an assemblage of six species (Nantahala River) in the Nantahala Mountains just west of Coweeta Creek. In these assemblages, age at first reproduction and fecundity are greater in the larger, more aquatic species. Instantaneous mortality rate is lower in the larger species; however, the latter have lower survival to first reproduction than the smaller species because developmental time to sexual maturation is lengthier than in the smaller species. Among species, it appears that size-mediated tradeoffs exist among age at sexual maturation, fecundity, and survival. The tradeoff relationships of life-history traits among species in both the Cowee and Nantahala assemblages may reflect fitness invariance or symmetry, perhaps stemming from design constraints in the genus *Desmognathus*. What remain unclear are factors contributing to the correlation between body size and the position of species along the stream-to-forest habitat gradient.

THE evolution of life histories is constrained by tradeoffs among such traits as survival, age at first reproduction, fecundity, propagule size, growth, and body size (Roff, 2002). The first three of these constitute direct fitness traits that enter into the characteristic equation, ${}_{x=\alpha}\Sigma^{\infty} l_x m_x e^{-rx} = 1.0$, where l_x and m_x represent survival to age x and number of female offspring at age x, respectively, α is the age of first reproduction, and r is the intrinsic rate of population increase. In a stationary population the net reproductive rate, $R_0 = 1.0$ and $r = 0$; thus, $R_0 = {}_{x=\alpha}\Sigma^{\infty} l_x m_x = 1.0$. In the present study of *Desmognathus* salamanders, I examine interspecific variation in the direct fitness traits, survival, fecundity, and age at first reproduction, in relation to variation in adult body size in assemblages in the southern Blue Ridge Mountains of southwestern North Carolina.

The plethodontid genus *Desmognathus*, currently with 21 recognized species, has maximum species richness in the southern Appalachian Mountains, where small watersheds may support from three to six or seven species. Generally, with some exceptions, the larger species are more aquatic and the smaller more terrestrial. This body size/habitat trend is paralleled by trends in life-history variation (Bruce, 2011).

Survival in *Desmognathus* has been evaluated by Organ (1961) for five species in southern Virginia. He reported that survivorship increased from the larger, more aquatic species to the smaller, more terrestrial species; i.e., in the sequence *D. quadramaculatus, D. monticola, D. fuscus, D. orestes, D. organi*. Tilley (1968) revised Organ's survival estimates for *D. monticola* and *D. fuscus*, and found minimal differences between them. He and others (e.g., Castanet et al., 1996) questioned some of the assumptions underlying Organ's (1961) analysis. Later investigators examined survival in single species, including *D. fuscus* (Spight, 1967; Danstedt, 1975; Price et al., 2012), *D. ocoee* (Tilley, 1977, 1980), and *D. monticola* (Bruce, 1995).

In salamanders, the body size–fecundity relationship is often modeled as *ln follicle number = ln a + b·ln standard length*, where follicle number represents a count of yolked ovarian follicles (e.g., in *Desmognathus,* Tilley, 1968; Jones, 1986; Bruce, 1996). The expected value of b is 3.0, inasmuch as follicle number represents a volume and standard length a linear dimension. This relationship should hold if growth is isometric and if egg size is constant (Roff, 2002:198–199). An increase in egg size as body size increases may increase survival through enhanced provisioning of the offspring, but will damp the body size–fecundity regression, such that the regression coefficient is < 3.0, unless reproductive effort is also increased. However, the gain in survival may more than offset any loss in fecundity.

Tilley (1968) analyzed the body size–fecundity relationship in several species of *Desmognathus*, based mainly on Organ's (1961) Virginia samples. Other data on the size–fecundity relationship have been provided by Harrison (1967) for *D. aeneus*, Jones (1986) for *D. santeetlah* and *D. conanti*, and Bruce (1996) for several species.

Age at first reproduction has been estimated for numerous species of *Desmognathus* (see Tilley and Bernardo, 1993:table 1). Skeletochronological estimates of age structure for three of the five species considered herein were provided by Castanet et al. (1996) and Bruce et al. (2002). For the remaining two species development to reproductive age was determined by analysis of body size distributions (Hining and Bruce, 2005; Bruce, 2009).

In my 1996 paper on life-history symmetry of species that occur in the Wolf Creek and Coweeta Creek watersheds in southwestern North Carolina, I suggested that instantaneous mortality rates were very similar among species, and assumed the values to be equivalent in the analysis of each assemblage. More precise estimates of age at first reproduction in the Coweeta assemblage (Bruce et al., 2002) and additional data on other life-history traits in these and nearby assemblages (Hining and Bruce, 2005; Bruce, 2009, 2010), as well as recent life-history data presented herein, necessitate a revision of the earlier mortality estimates. Thus, one objective of the present paper is to test the null hypothesis that instantaneous mortality rates are equivalent in the several species that co-occur in the assemblages in

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question. A second objective is to compare the findings with published estimates of mortality/survival in *Desmognathus*. Finally, I examine how tradeoffs among species in mortality, age at first reproduction, fecundity, and body size in the assemblages in question may inform our understanding of the evolutionary ecology of the genus.

MATERIALS AND METHODS

All localities lie within the southern Blue Ridge Physiographic Province in southwestern North Carolina, USA. The Cowee Mountain locality includes the watershed of Wolf Creek, which drains Cullowhee Mountain, a spur of the Cowees in Jackson County. All three species of the assemblage (*D. quadramaculatus, D. monticola, D. ocoee*) were sampled at Wolf Creek. Two assemblages were sampled in the Nantahala Mountains: (1) Coweeta Creek, at Coweeta Hydrologic Laboratory, in Macon County; and (2) the upper sections of the Nantahala River watershed, including Kimsey Creek, Park Creek, and Little Rock Branch, also in Macon County. All five species of the Coweeta Creek assemblage (*D. quadramaculatus, D. monticola, D. ocoee, D. aeneus, D. wrighti*) were sampled there, but only the last three at the Nantahala River sites.

Many of the data in this paper are summarized from earlier studies of the Cowee and Nantahala populations (Bruce, 1990, 1996, 2009, 2010; Castanet et al., 1996; Bruce et al., 2002; Hining and Bruce, 2005). For the newer data, measurements of standard length (SL) were taken to the nearest 0.1 mm from the tip of the snout to the caudal end of the cloacal slit on living salamanders, anesthetized in MS-222. The females were then fixed in 10% formalin and eventually transferred to 70% ethyl alcohol. I counted yolked follicles (NFOL) in the ovaries of females wherein the diameters of the majority of such follicles were ≥ 1.5 mm in *D. ocoee*, *D. aeneus*, and *D. wrighti*, and ≥ 2.0 mm in *D. quadramaculatus* and *D. monticola*. I log-transformed both variables and regressed ln NFOL on ln SL.

Instantaneous mortality rates were estimated by solving the characteristic equation, ${}_{\alpha}\Sigma^{\omega} l_x m_x e^{-rx} = 1.0$, summed from the age ($x$) at first reproduction ($x = \alpha$) to final reproduction ($x = \omega$), under the assumption that the population is stationary, with a population growth rate, $r = 0$. Under this condition $R_0 = {}_{\alpha}\Sigma^{\omega} l_x m_x = 1.0$. A second assumption was that the instantaneous mortality rate, M, was a constant in each population. This allowed the l_x variable to be calculated as e^{-Mx}.

The assumption of a stationary population is supported by the observation that both principal localities support mature deciduous forests that have undergone no recent major disturbances. The Wolf Creek watershed was obtained by Western Carolina University in 1957–1959 for watershed protection, and was undisturbed through the 1980s and 1990s when my field work was carried out. Moreover, the studies of Hairston (1996), Dixon and Pechmann (2005), and Warren and Bradford (2010) indicated that populations of four species of *Desmognathus* at Coweeta Hydrologic Laboratory were stable from 1976 through 2007, which encompasses most of the period in which my studies were conducted. (*Desmognathus wrighti* is uncommon at Coweeta, is restricted to higher elevations, and was not included in those surveys.)

In Roff's life history analysis of teleost fishes (Roff, 1984, 2002), he modeled survival according to $l_x = pe^{-Mx}$, where p is the probability of surviving through the larval stage, wherein egg and larval mortality is usually very high in fishes. In my analysis of *Desmognathus*, I have assumed a constant instantaneous rate of mortality throughout life, i.e., $l_x = e^{-Mx}$. A constant instantaneous mortality rate yields a Type II survivorship curve, in which a plot of the logarithms of number of survivors of an original cohort, i.e., the logarithms of the l_x values against age, x, is a straight line. To justify this approach, in *Desmognathus*, in contrast to most fishes, fecundity is much lower and females brood their clutches until hatching. Thus, differentials in rates of mortality between egg/larval stages and later stages may be much less than in fishes and other organisms. Although it is likely that within a species there is variation in survivorship over the course of the life span, the incorporation of a constant instantaneous mortality rate averages out such variation under the assumption of $R_0 = 1.0$, and thereby provides a metric for comparisons among species. In solving the characteristic equation for instantaneous mortality rate, M, I used the Solve routine of Mathematica, which iterates a solution using inverse functions.

RESULTS

To estimate female survival to reproductive age, I solved the characteristic equation for instantaneous mortality rate (M) from the available data on annual fecundity and age at first reproduction. A summary of age at first reproduction, body size, and fecundity in adult females of the Wolf Creek, Coweeta Creek, and Nantahala River populations of *Desmognathus* is provided in Table 1. In *D. quadramaculatus* and Wolf Creek *D. monticola* there was no trend for follicle number to increase with SL; this was ostensibly a result of small sample sizes, narrow ranges of adult female body size, and high residual variances in follicle number. Moreover, although the size–fecundity relationship could not be reliably evaluated in *D. aeneus* and *D. wrighti* because of small sample sizes, adult females of both species showed narrow ranges of body sizes. However, in all three samples of *D. ocoee* (Fig. 1) and the small sample of Coweeta *D. monticola* (Fig. 2) the regressions of ln NFOL on ln SL were significant (Table 2). The difference between *D. ocoee* and other species may stem from a relatively greater range of SL in gravid females of the former. With the exception of the small sample of Coweeta *D. wrighti*, this difference is reflected in the greater coefficients of variation (CV) of standard length of gravid *D. ocoee* versus the other species (Table 1).

On the basis of the above findings, initially, for each population of each species, the annual fecundity or m_x variable was assumed constant for mature females over their reproductive life span, and was calculated from the mean follicle counts of gravid females (Table 1), divided by 2, to estimate female eggs/female (model 1). In addition, for Wolf Creek and Coweeta *D. ocoee,* and Coweeta *D. monticola,* I used the regression of ln NFOL on ln SL, estimating age-specific standard lengths, SL_x, from Gompertz growth equations (Table 2). Thus, for these populations, female eggs/female, $m(x) = (a[SL_x]^b)/2$ (model 2). This procedure could not be used for the Nantahala population of *D. ocoee* because the relevant age data for calculating the Gompertz equation were not available.

In estimating M values I used the modal age at first reproduction, α, and extended the summation for four years beyond α, i.e., five reproductive seasons. Extension to later ages had only minor effects on M. In females of *D.*

Table 1. Body Sizes and Follicle Counts of Gravid Females. Modal ages at first reproduction (α) from Castanet et al. (1996) and Bruce et al. (2002).

Assemblage Species	Modal α (yr)	*n*	SL (mm)				Yolked follicles		
			Range	Mean	SD	CV	Range	Mean	SD
Wolf Creek									
D. quadramaculatus	8	14	71–85	78.5	4.26	5.43	42–61	52.1	5.94
D. monticola	6	23	56–65	60.2	2.40	3.99	19–39	29.0	5.58
D. ocoee	4	24	31–41	35.9	3.28	9.13	9–22	15.0	3.64
Coweeta									
D. quadramaculatus	9	6	84–93	87.1	3.37	3.87	38–69	55.5	11.0
D. monticola	6	11	60–70	65.0	3.47	5.34	22–44	28.1	6.64
D. ocoee	4	16	34–46	40.4	3.33	8.24	12–28	16.9	4.04
D. wrighti	3	4	25–30	26.7	2.40	8.99	8–10	9.3	0.96
D. aeneus[a]	3	13	23–28	26.3	1.45	5.51	8–14	11.7	2.25
Nantahala									
D. ocoee	4	39	33–50	40.1	3.60	8.98	10–30	16.5	4.71
D. aeneus	3	7	25–28	26.5	0.95	3.58	10–14	11.7	1.25

[a] Follicle counts of Coweeta *D. aeneus* were made on only 6 of the 13 gravid females.

quadramaculatus the most frequent ages at first reproduction were eight years at Wolf Creek (Castanet et al., 1996) and nine years at Coweeta (Bruce et al., 2002). At both localities the most frequent ages at first reproduction in females reported in the preceding studies were six years in *D. monticola* and four years in *D. ocoee*. In the southern Nantahalas females of *D. aeneus* and *D. wrighti* both reproduce initially at three years (Hining and Bruce, 2005). Incorporating these α values and the fecundity and growth data of Tables 1 and 2 provided the estimates to solve the model 1 and 2 equations for *M*:

$$\text{Model 1}: {}_{x=\alpha}\Sigma^{\omega} m_x \cdot exp(-M \cdot x) = 1.0.$$

$$\text{Model 2}: {}_{x=\alpha}\Sigma^{\omega}\left(\left(a \cdot (SL_0 \cdot exp((\beta/\alpha) \cdot (1 - exp(-\alpha \cdot x))))^b\right)/2\right) \cdot exp(-M \cdot x) = 1.0.$$

The results for the two models are given in Table 3. Thus, in both assemblages the model 1 analyses suggested that instantaneous mortality rate decreases as body size increases across species, but, because larger species are older at first reproduction, survival to the age at first reproduction is lower in larger species. For the species/populations where the model 2 analysis was applied, the estimates were similar to those of model 1, and did not affect the among-species trend.

DISCUSSION

Studies of survivorship in *Desmognathus*, generating survivorship curves and/or life tables, have been conducted by Organ (1961) for five species, Spight (1967) for *D. fuscus*, Tilley (1968) for *D. fuscus* and *D. monticola*, Danstedt (1975) for several populations of *D. fuscus*, Tilley (1980) for two populations of *D. ocoee*, Bruce (1995) for *D. monticola*, and Price et al. (2012) for *D. fuscus*. Organ's (1961) analysis indicated that larval/juvenile survival increases in the sequence *D. quadramaculatus, D. monticola, D. fuscus, D. orestes,* and *D. organi*, i.e., from the largest to the smallest species. However, for older individuals differences in survival among species were less evident (e.g., Organ, 1961:fig. 8). In contrast, my survival estimates, averaged over the entire life spans, suggested that survival decreases from the largest to the smallest species in both the Cowee and Nantahala Mountain assemblages.

Organ's, Spight's, and Danstedt's survival estimates were all based on analyses of size-frequency distributions, counts of testis lobes, and sex ratios. These methodologies undoubtedly introduced errors into the survival estimates, as noted by Tilley (1977) and Castanet et al. (1996). Moreover, Organ's contention that in all five species ages at sexual maturation were identical across species' boundaries (males: 3.5 yr; females: 4.5 yr, followed by first reproduction at 5.0 yr) are suspect. Studies of other populations/species have shown that larger species of *Desmognathus* are older at reproductive maturity (Tilley and Bernardo, 1993:table 1; Castanet et al., 1996; Bruce et al., 2002). Thus, developmental rates to sexual maturity, ages at first reproduction, and survival in the Virginia populations studied by Organ require re-examination.

A Jolly-Seber multiple-recapture methodology was employed over a seven-year period by Tilley (1980) to investigate survivorship in a lower and a higher elevation population of *D. ocoee* in the southern Blue Ridge of North Carolina. He estimated survival from hatching to first reproduction at four years as 0.087 (low elevation) and at five years as 0.059 (high elevation). At a constant instantaneous rate of mortality, these represent annual survival rates of 0.610 and 0.566 in the lower- and higher-elevation populations, respectively. For adults, Tilley estimated annual survival rates of 0.626 and 0.743 in the lower- and higher-elevation populations. For these populations the R_0 values calculated from the life tables were 1.03 and 1.29, respectively. The survival estimates are similar to my results for *D. ocoee*.

The use of a capture–mark–recapture method in *D. fuscus* in the Piedmont of North Carolina by Price et al. (2012) yielded annual survival estimates of adults of 0.216 in an undisturbed stream and 0.036 in a recently disturbed stream. The former is less than Danstedt's (1975) estimates (0.238–0.426) for adults in several populations of this species. Spight's (1967) study of *D. fuscus* in a population near those sampled by Price et al. (2012) also yielded a

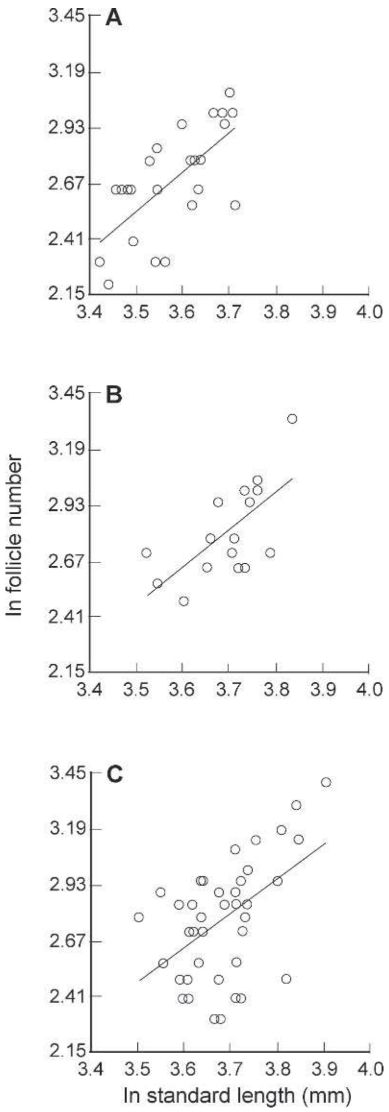

Fig. 1. Regressions of ln follicle number on ln standard length for *Desmognathus ocoee*. (A) Wolf Creek. (B) Coweeta. (C) Upper Nantahala River.

higher estimate of annual adult survival (≈0.340) than that recorded by Price et al. for their undisturbed population, but was based on an analysis of age structure that is difficult to interpret (Spight, 1967:table 1).

My investigation (Bruce, 1995) of *D. monticola* using temporary removal sampling generated annual survival estimates of 0.5–0.6, similar to those reported herein for this species. In a subsequent study of Coweeta and Wolf Creek *Desmognathus* I assumed equivalent instantaneous mortality rates among species (Bruce, 1996); however, more precise estimates of age at first reproduction in the Coweeta species (Bruce et al., 2002), and the additional data on female body size and fecundity, have necessitated revision of the earlier estimates of mortality. In the 1996 study I calculated regressions of ln follicle number against ln SL for the pooled data of the three species at Wolf Creek and four of the five species at Coweeta (Bruce, 1996:fig.1). The regression coefficients (Wolf Creek: 1.459, Coweeta: 1.405) were less than the predicted value of 3.0, which I ascribe, in part, to the larger eggs of the larger species; i.e., a tradeoff between egg size and egg number. Unfortunately, there are currently inadequate data on egg size for one or more species in each of the assemblages to test this hypothesis.

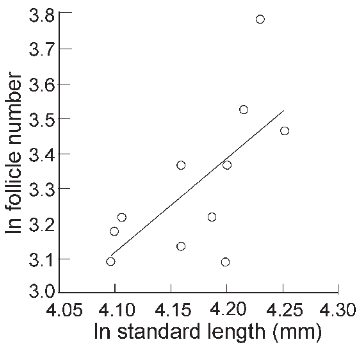

Fig. 2. Regression of ln follicle number on ln standard length for Coweeta *Desmognathus monticola*.

Organ (1961) and Danstedt (1975) assumed that the species/populations they studied were stationary (R_O = 1.0). My estimates of mortality/survival require the assumption of stationary populations with stable age distributions (R_O = 1.0, r = 0) over the period in which sampling was conducted. Long-term relative stability of several species of *Desmognathus* is documented for Coweeta (Hairston, 1996; Dixon and Pechmann, 2005; Warren and Bradford, 2010). Moreover, most of the forested watersheds at Coweeta had been undisturbed for several decades prior to my studies. Likewise, at Wolf Creek the forest had undergone no major disturbance for many years prior to and throughout the study period. Assuming the reliability of the age and fecundity data, the estimates of annual mortality and survival to age at first reproduction in these populations generate a pattern in which larger species attain their larger sizes mainly by delaying reproduction, which, despite lower instantaneous mortality rates, lowers their probability of survival to reproductive maturity, but generates gains in fecundity. Thus, larger adult size may enhance the survival rate of embryos, larvae, and juveniles to adulthood by allowing a greater investment in provisioning of the offspring and by providing more effective parental care of eggs by the larger brooding female. In contrast, although smaller species have higher mortality rates and lower fecundity, by accelerating development they achieve a higher rate of survival to reproductive age than the larger species. These relationships constitute a pattern of size-mediated tradeoffs in direct fitness traits in the genus.

How this pattern of life-history tradeoffs relates to that of habitat segregation by body size in the genus remains unclear, in particular the influence of intraguild interactions (intraguild predation, interspecific competition), as analyzed by Hairston (1986) and others (reviewed in Wells, 2007; Bruce, 2011), versus the role of such factors as habitat structure, resources, predators, and competitors along the gradient from stream to forest. The untangling of these influences remains a challenge to a full understanding of the evolutionary ecology of *Desmognathus*.

Hubbell (2001) referred to predictable covariance of life-history traits along the body-size gradient of an assemblage of related species as fitness invariance; he suggested that such invariant relationships reflect design constraints of the species involved. Such a model may be applicable in *Desmognathus*. Aside from the disparity in adult body size, wherein large adults of *D. quadramaculatus* (≈25 g) are about 50 times as massive as large adult *D. aeneus* and *D. wrighti*

Table 2. (A) The Body Size–Fecundity Relationship in Three Populations of *Desmognathus ocoee* and Coweeta *D. monticola* According to the Equation $\ln NFOL = \ln a + b \cdot \ln SL$, where $NFOL$= follicle number in gravid females and SL = standard length in mm. r^2 = coefficient of determination. (B) Gompertz equations for growth in standard length, $SL_x = SL_0 \cdot \exp((\beta/\alpha)\cdot(1-\exp(-\alpha \cdot x)))$, where SL_0 = standard length at hatching and x = age in years.

Population	n	(A) Regression equation	P	r^2
D. monticola				
Coweeta	11	$\ln NFOL = -7.816 + 2.667 \ln SL$	0.025	0.445
D. ocoee				
Coweeta	16	$\ln NFOL = -3.499 + 1.706 \ln SL$	0.006	0.433
Nantahala	39	$\ln NFOL = -3.068 + 1.582 \ln SL$	0.001	0.254
Wolf Creek	24	$\ln NFOL = -3.892 + 1.838 \ln SL$	<0.001	0.453
		(B) Gompertz equation		r^2
D. monticola				
Coweeta[a]	111	$SL_x = 11.8\exp((0.642/0.333)(1-\exp(-0.333x)))$		0.920
D. ocoee				
Coweeta[b]	101	$SL_x = 9.24\exp((0.696/0.388)(1-\exp(-0.388x)))$		0.891
Wolf Creek[c]	76	$SL_x = 9.44\exp((0.648/0.377)(1-\exp(-0.377x)))$		0.829

[a] From Bruce (2010).
[b] From Bruce (2009).
[c] Calculated from data in Castanet et al. (1996).

(≈0.5 g; Bruce, unpubl. data), there is otherwise only minor variation in morphology among species (Sweet, 1973, 1980) that may reflect design constraints in the skeleto-muscular specializations for feeding and head wedging that distinguish *Desmognathus* (and *Phaeognathus*) from other plethodontids (Schwenk and Wake, 1993).

I suggest that within the limitations prescribed by morphological design constraints, diversification in *Desmognathus* has yielded species that have undergone niche differentiation and community assembly that is characterized by predictable size-mediated covariance in the direct fitness traits considered herein, i.e., age at first reproduction, fecundity, and survival, as well as in such other traits as egg size (Tilley and Bernardo, 1993:table 1; Beachy, 1993:table 1) and the larval period (Bruce, 2011:table 1). Occasionally, lineages of desmognathines—usually short-lived—may have arisen that escaped such design constraints, and pursued new evolutionary trajectories; e.g., as reflected in the ecological and life-history adaptations of the extant *Phaeognathus hubrichti* (Dodd, 2005). Given that a common pattern of geographic variation in existing assemblages of *Desmognathus* involves larger species that are more aquatic and smaller species that are

Table 3. Estimated Mortality Rates of Wolf Creek and Coweeta *Desmognathus*. Models 1 and 2 are described in text.

Assemblage Species (model)	Female age at first reproduction (yr)	Female eggs per female	Annual mortality rate	Survival to α
	α	Mean	M	$e^{-M\alpha}$
Wolf Creek				
D. quadramaculatus (1)	8	26.04	0.512	0.017
D. monticola (1)	6	14.48	0.574	0.032
D. ocoee (1)	4	7.52	0.674	0.067
(2)	4	–	0.704	0.059
Coweeta				
D. quadramaculatus (1)	9	27.75	0.467	0.015
D. monticola (1)	6	14.05	0.569	0.033
(2)	6	–	0.577	0.031
D. ocoee (1)	4	8.45	0.698	0.061
(2)	4	–	0.705	0.060
D. wrighti (1)	3	4.63	0.724	0.114
D. aeneus (1)	3	5.84	0.785	0.095
Nantahala				
D. ocoee (1)	4	8.25	0.692	0.063
D. aeneus (1)	3	5.86	0.786	0.095

more terrestrial (Bruce, 2011), the pattern may represent an early and persistent aspect of the history of the genus that subsumes specific episodes of speciation, vicariance, dispersal, and extinction.

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