

ARTICLES

Age at Maturation, Body Size, and Life-History Evolution in the Salamander Family Plethodontidae

Tilley and Bernardo (1993) have done herpetologists a great service in their review of life history evolution in the salamander family Plethodontidae. They are quite correct in their interpretation that our current understanding of plethodontid life history evolution is based more on traditional viewpoints (e.g., Dunn 1926) than on real data. My intent in this paper is to supplement their suggestions on research directions in this family of salamanders.

What are the Important Aspects of Plethodontid Life Histories?

Because body size affects nearly every aspect of plethodontid evolutionary ecology (e.g., Hairston 1987; Tilley and Bernardo 1993), I will focus on this key trait. I will argue that the primary influences on interspecific and intraspecific variation in body size are duration of the larval period and juvenile period.

My arguments require several assumptions. First, while there are good reasons not to ignore the effects of egg size (e.g., Bernardo 1991a, 1994), I do so only to simplify my arguments. Second, I assume that growth after maturation contributes negligibly to interspecific variation in adult body size. At least for females, a significant component of energy formerly dedicated to growth is allocated to reproduction after maturity is attained (Hom 1988; Tilley 1980). This assumption may have less validity for males (Bruce 1993; Tilley 1980).

Egg size effects aside, there are only four ways to change body size in an amphibian: change (1) larval growth rate; (2) juvenile growth rate; (3) duration of the larval period; and (4) duration of the juvenile period. I will argue that variation in plethodontid life histories is due primarily to the latter two, and variation in growth rate contributes negligibly to variation in life histories.

For example, *Desmognathus monticola* attain a larger body size as adults than do *D. ochrophaeus* (Organ 1961). They do so primarily by extending the length of the juvenile period; growth rate and egg size play less important roles (Bruce 1990). The result is an additional year of growth prior to maturity, with all the correlated effects, e.g., increased clutch size and egg size (Bernardo 1994; Tilley 1968). Extending the comparison to the largest species in the genus, *D. quadramaculatus*, the larger size of this species seems to be due to an increase in larval period, relative to *D. monticola* and *D. ochrophaeus* (Bruce 1988a).

Changing the duration of the larval or juvenile period can also explain intraspecific variation in adult body size. Tilley (1973) specifically ascribed large body size of high elevation *D. ochrophaeus* (relative to low elevation conspecifics) to delayed maturity. The growth curves of Tilley (1980) document that the larger size of high elevation individuals is due to an additional year of growth as juveniles, with variation in growth rate contributing little to the difference in adult body size. In an elegant study, Bernardo (1994) convincingly demonstrated that this life history variation is due to genetic difference in maturation age and that growth potential does not differ between these populations.

In order to determine whether this trend is a general one for the desmognathines, I used the data that Tilley and Bernardo pro-

vided (their Table 1) to calculate approximate growth rates and evaluate the degree of interspecific variation in this trait (these rates should not be regarded as estimates of growth rate in natural populations). These rates are presented in Table 1.

As a test of the utility of these estimates, I constructed a table that listed the contributions of hatching size, growth rates, and age at maturation to the difference in adult body size between *D. monticola* and southern *D. ochrophaeus*. This table was compared with that listed in Bruce (1990)—who used real animals—and the differences between my estimates and Bruce's appeared to be small enough (Table 2) to allow interpretation of growth rate data of Table 1. (Because Tilley and Bernardo's table used Bruce [1990], I removed any data attributable to this reference so that the estimates presented in Table 2 were as independent as possible. Thus, in constructing Tables 1 and 2, I used Juterbock [1984] as my primary reference for *D. monticola*. However, the only estimate of minimum age at maturity for this species is found in Bruce [1990]. Thus the two data sets present in Table 2 are not completely independent.)

TABLE 1. Rates of growth estimated from Tilley and Bernardo (1993). Larval growth rate is calculated as

$$\frac{(\text{size at metamorphosis} - \text{hatching size})}{(\text{age at metamorphosis})}$$

Juvenile growth rate is calculated as

$$\frac{(\text{size at maturity} - \text{size at metamorphosis})}{(\text{age at maturity} - \text{age at metamorphosis})}$$

Data are medians taken from Tilley and Bernardo. *Desmognathus aeneus* and *D. wrighti* are direct-developers (Collazo and Marks 1989; Harrison 1967; Organ 1961; Wake 1966).

Species	larval growth rate (mm SVL/mo)	juvenile growth rate (mm SVL/mo)
<i>Desmognathus quadramaculatus</i>	0.62	0.67
<i>Leurognathus marmoratus</i>	0.59	1.08
<i>Desmognathus monticola</i>	0.30	0.80
<i>Desmognathus fuscus</i> (northern)	0.63	1.17
<i>Desmognathus ochrophaeus</i> (southern)	0.40	0.54
<i>Desmognathus aeneus</i>	—	0.48
<i>Desmognathus wrighti</i>	—	0.40

The growth rates do not differ dramatically across taxa in the way one would expect if variation in growth rate is a significant component of interspecific variation in body size (Table 1). In addition, I used the growth rates present in Table 1, and the data on minimum SVL at maturity and minimum age at maturity from Tilley and Bernardo, to generate Pearson correlation coefficients among these traits. Larval growth rate was not correlated with SVL at maturity ($r = 0.36$, $df = 3$, $P > 0.05$); nor was juvenile growth rate ($r = 0.59$, $df = 5$, $P > 0.05$). However, age at maturity was positively correlated with SVL at maturity ($r = 0.77$, $df = 5$, $P < 0.05$). Thus, it appears that variation in body size in desmognathine salamanders is most related to variation in maturation age. Maturation age is simply a function of the duration of the larval and juvenile periods.

Does this pattern hold for the other groups of the plethodontids, i.e., the tribes Plethodontini, Bolitoglossini, and Hemidactyliini of the subfamily Plethodontinae? As noted by Tilley and Bernardo, there is little information concerning life histories in the

Plethodontini and Bolitoglossini, but dramatic variation in several species of the Hemidactyliini has been well documented and suggests that the trend for the desmognathines also holds for the hemidactyliines.

For example, the hemidactyliine *Gyrinophilus porphyriticus* in the southern Appalachians exhibits variation in age at maturation. In the Cowee, Nantahala, Balsam, and southern Blue Ridge Mountains, the larval period is 3–5 yr (Bruce 1980). In the Nantahala and Balsam Mountains and Cowee Mountains northwest of Watauga Gap, *G. porphyriticus* individuals follow metamorphosis with a one year juvenile period, whereas those from the southeast Cowee Mountains and southern Blue Ridge Mountains are mature at metamorphosis (Bruce 1972, 1978). The result of this accelerated maturation is smaller animals. Further, *G. porphyriticus* from the Great Smoky Mountains metamorphose at a small size (suggestive of a short larval period) but mature at a size comparable to the Northwest Cowee, Nantahala, and Balsam Mountain populations, suggesting an extended juvenile period (Bruce, unpubl. data). This indicates that geographic differences in adult body size in *G. porphyriticus* are due to variation in larval period and juvenile period.

Thus, a key question for researchers involves the relationship between larval period and juvenile period. A relationship usually exists between age at metamorphosis and age at maturation. However, the correlation is usually a spurious one: paedomorphs notwithstanding, a long larval period is accompanied by a delay in maturation. There may be no correlation between length of the juvenile period and length of the larval period (for the species of Table 1: $r = -0.23$, $df = 5$, $P > 0.05$). While this analysis is based on only a few data, it suggests the hypothesis that age at maturation and age at metamorphosis are free to evolve independently. Previously, Bruce (1989) suggested that the two factors are not tightly linked in desmognathine salamanders. The presence of paedomorphic hemidactyliines further supports this hypothesis.

I suggest that the evolution of body size in plethodontids is largely a result of changes in age at metamorphosis and maturation. I believe that a focus on questions that address variation in larval period and/or juvenile period is most likely to result in informative work. A critical way to address these questions is to generate mortality schedules.

Mortality Schedules and Life History Evolution in Plethodontids

What are the causes of variation in age at maturation in the plethodontid salamanders? All other factors being held equal, life histories evolve when mortality schedules are varied (Charlesworth 1980; Schaffer 1974). For example, Charlesworth (1980) showed that when a delay in reproduction is associated with an increase in fecundity, e.g., via an increase in body size (the case for salamanders [Kaplan and Salthe 1979]), there is selection for delayed maturation when early age mortality is increased. Organ (1961) suggested the hypothesis that the mortality of more aquatic, stream-dwelling plethodontids (i.e., larger species) is higher early in life than in more terrestrial species (i.e., smaller species). If this hypothesis is correct, then high early life mortality can explain delayed maturation and large body size in aquatic plethodontids.

Viewed in this context, the need for clear mortality schedules is outstanding. Currently, there are schedules of survival for only four species of plethodontids: *D. ochrophaeus* (Tilley 1980), *D. fuscus* (Danstedt 1975; Spight 1967), *Plethodon jordani* (Hairton 1983), and *Eurycea wilderae* (Bruce 1988b). Some comparisons can be made among the life tables for these four species. For

example, Bruce (1988b) noted that the most aquatic species (*E. wilderae*) has the highest early life mortality and shortest mean generation time, and the most terrestrial species (the direct-developing *P. jordani*) has the lowest early life mortality and longest mean generation time.

TABLE 2. Comparison of two estimates of contributions to difference in adult body size between *Desmognathus monticola* and *D. ochrophaeus*. The estimate from this study is derived from median data taken from Tilley and Bernardo (1993). To facilitate this comparison the juvenile growth rate of *D. monticola* was assumed to be constant.

Source of difference	Bruce (1990)		This study	
	SVL (mm)	%	SVL (mm)	%
Hatchling size	2.4	13.8	3.20	15.6
Age at maturation	11.5	66.1	13.45	65.6
Growth	3.5	20.1	3.85	18.8
Total	17.4	100.0	20.50	100.0

However, more meaningful interpretations will result from life tables of groups of species that are closely related. For example, Organ (1961) provided life tables for five species of desmognathines that suggested that the more aquatic species suffer higher mortality early in life than species that are more terrestrial. However, Organ suggested that all the species he studied matured at the same time, and there is basis for reconsideration of his estimates (e.g., Bruce 1989).

In generating their life tables, these workers assumed that mortality in mature plethodontids is constant. A useful study would be one that tests this assumption, and new techniques for estimating the age of individuals (e.g., osteochronology [Houck and Francillon 1988]) would help in this evaluation.

Age at Maturation and Adaptive Radiation?

While age at maturation is the primary determinant of adult body size in plethodontids, how is it related to other aspects of plethodontid evolution? I suggest that variation in age at maturation is related to, at least, two phenomena that are important aspects of adaptive radiation: speciation and specialization.

Bernardo (1991b) has suggested that because body size influences the distance moved after deposition of a spermatophore (Arnold et al. 1993), divergence in body size between populations can result in sexual isolation. There appears to be significant sexual isolation between the northwest and southeast Cowee Mountain populations of *Gyrinophilus porphyriticus* and this isolation appears to be due to population divergence in body size via differences in age at maturation (Beachy, *in press*). It seems tenable that much of the species diversity of the family is due to evolution of body size and the unique tail-straddle walk of the plethodontids.

Phyletic shifts in body size have been associated with, and may be a cause of, major ontogenetic changes that produce profound new morphologies in amphibians (Hanken 1989). A spectacular example of how change in body size affects morphology, behavior, and ecology is the tropical plethodontid genus *Thorius* (Hanken 1982, 1985).

Researchers often avoid the “tedious” tasks of elucidating life histories and mortality schedules. The work is usually time-consuming and descriptive (problematic for the graduate student looking to make a breakthrough during a time when the power of the

ecological experiment has been fully appreciated [e.g., Hairston 1986; Wilbur 1987]). However, commitment to this descriptive program will provide important insights to plethodontid evolutionary ecology. For at least the *Desmognathinae* and *Hemidactyliinae* (the less derived of the four major groups of plethodontids), shifts in maturation age (and sometimes metamorphic age) seem to be the dominant correlate with changes in body size. If changes in body size in plethodontids are due primarily to changes in age at maturity, then the study of life histories is intricately bound with morphology, ecology, and adaptive radiation in, this, the most successful group of caudate amphibians.

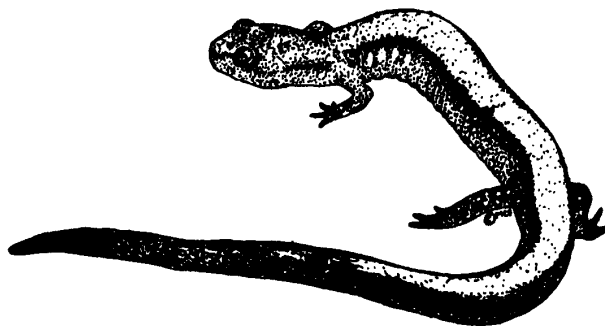
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Plethodon cinereus (Red-backed Salamander). USA: Massachusetts: Reading. Illustration by Mark C. Erelli.