Life-History Perspective of Adaptive Radiation in Desmognathine Salamanders

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This study investigates interspecific variation in age at first reproduction, fecundity, and body size in multispecies assemblages of desmognathine salamanders. The hypotheses tested are *that interspecific differences in body* size *among* desmognathines stem proximately from variation in age at first reproduction and that variation in the latter trait is positively correlated with variation in fecundity among species. It is shown that a correlation between age at first reproduction and fecundity, combined with a uniform rate of survival, based on available estimates of these parameters, will yield equivalent values of net reproductive rate (R_o) among the species of a given assemblage. Such equivalence represents a form of life-history symmetry. Data from two assemblages are presented in support of the argument for symmetry. Such life-history symmetry may reflect uniformity in morphological specialization in desmognathines. Given the morphological adaptations to burrowing (had-wedging) in the subfamily, the relationship between adult body size and habitat preference in *Desmognathus* may reflect adaption to the size of cover objects *and composition of the substratum* along the aquatic-terrestrial habitat gradient I propose that these variables, in association with predation and competition, represent the selective factors responsible for body size diversification in *Desmognathus.*

FEW genera of vertebrates exhibit variation in body size and life history as extreme as that shown by the dusky salamanders of the genus *Desmognathus* (Tilley and Bernardo, 1993). *Desmognathus,* with 16 species currently recognized, is the principal genus in the subfamily Desmognathinae, that otherwise contains only the monotypic *Phaeognathw* (Tilley and Mahoney, 1996; Titus and Larson, 1997). The subfamily represents a-highly derived, monophyletic lineage within the Plethodontidae (Schwenk and Wake, 1993).

In contrast to the pronounced variation in size and life history, desmognathines are morphologically conservative (Wake, 1966; Sweet, 1973, 1980). Synapomorphies that distinguish the desmognathines from other salamanders include nine skeletomuscular characters related to feeding and/or burrowing (Schwenk and Wake, 1993). Although desmognathines are essentially semiaquatic streamside salamanders, an extensive adaptive radiation in the southern Appalachian Mountains has yielded fully aquatic and terrestrial species. What is remarkable about this radiation is the nearly exact correlation between body size and life history-the larger forms are more aquatic, the smaller are more terrestrial (Hairston, 1949). The physiographic setting for the adaptive radiation has been the broad moisture gradient of the humid montane forests of the southern Appalachians. Competition (Hairston, 1949, 1973, 1986) and predation (Tilley, 1968; Hairston. 1986) may represent the factors that regulate the observed

pattern of species dixriiucion along the moisture gradient.

Phaeognathus hubrichti, the largest species in the subfamily, is the only important exception to the body size-habitat correlation. It is an elongate, terrestrial burrower endemic to southern Alabama_ Thus, the model presented herein is restricted to *Desmognathus. Phaeognathus* is excluded on the basis of extreme morphological specialization and absence from multispecies assemblages of the Appalachians.

It was originally hypothesized that the aquatic desmognathines are more primitive than the terrestrial forms. with evolution having proceeded unidirectionally or nearly so (Dunn. 1926; Hairston, 1949. 1985). More recently, Bruce (I 99 1) postulated that the ancestral mode of life is best represented by the semiaquatic, streamside species, such as *D. fuscus,* with both the aquatic and terrestrial life histories representing derived states. Tilley and Bernardo (1993) subsequently questioned long-standing assumptions relating life-history variation in extant species to the phylogenetic history of desmognathines. They argued that ecological constraints observed in desmognathine assemblages, acting with life-history and morphological covariafion, could serve to decouple observed trends in life history from phylogeny. In the same year, Schwenk and Wake (1993), in elucidating the terrestrial feeding mechanism of the aquatic *D. marmoratus,* suggested that adult desmognathines have secondarily invaded stream habitats. Molecular data even suggest that the fully terrestrial species represent the basal condition (Titus, 1992; Titus and Larson. 1997; see also Collazo and Marks, 1994). Confirmation of this hypothesis would rquire the demonstration chat desmognathines have reevolved the larval stage. Thus, the traditional view of desmognathine evolution is under challenge by newer data from a variety of sources.

An unresolved evolutionary problem is how a morphologically conservative lineage like the desmognathines (Sweet. 1980) has undergone such extreme diversification in body size and life history to yield the observed aquatic-terrestrial gradient in species distribution in the southern Appalachians. In this paper, I offer a solution that is predicated on the hypothesis that morphological uniformity within the subfamily is associated with common demography. The demographic model outlined below, which is an elaboration of ideas presented earlier (Bruce, 1995:411), is evaluated with data from two desmognathine assemblages.

Demographic model.-Body size in *Desmognathus* in the southern Appalachian Mountains covaries with habitat association. Small species are terrestrial and large ones are aquatic (Hairston, 1949, 1980, 1987). Interspecific variation in body size within an assemblage is explained by variation in egg size, growth, and age at first reproduction, with the last accounting for most of the variation (Bruce, 1990). In a given assemblage, the increase in age at first reproduction (α) is ordinarily one year in each step of the series (Castanet et al., 1996).

In some assemblages, average annual fecundity (b) nearly doubles as body size increases in each step in the sequence of species (Bruce, 1995). The ratio of average annual fecundity of a larger to the next smaller species is the fecundity multiplier, k.

Annual prereproductive survivorship is approximately 0.5–0.6 in each species (Tilley, 1980; Bruce, 1995). To maintain equivalence in net reproductive race (R_0) among species, the precise relationship between fecundity and annual survivorship (s) is $k = 1/s^*$, where k is the fecundity multiplier as age at first reproduction increases by a constant increment, n, in each step of the sequence. If $n = 1$ year, then $k = 1/s$.

If $R_0 = 1.0$ in a species, it will be maintained at 1.0 if the species evolves to a larger or smaller size through the mechanism of increasing or decreasing age at first reproduction. Because of these relationships, the species of a given assemblage are demographically uniform: i.e.. at a given body size individuals of different species are interchangeable in terms of survival probability and fecundity. Invariance in these life-history parameters represents a form of symmetry (Charnov, 1993).

As a consequence of demographic similarity. adjustments in age at first reproduction represent a mechanism for increasing or decreasing body size that does not involve a cost in fitness. Thus, body size is free to evolve, unconstrained by demographics, in response to a variety of selective factors.

MATERIALS AND METHODS

New data presented in this paper are follicle counts of gravid females and counts of deposited eggs in field clutches. Sampling localities were in the Wolf Cieek and Coweeta watersheds. Wolf Creek is a 141-ha tract on Cullowhee Mountain. a spur of the Cowee Mountains, in Jackson County, North Carolina. Most of the fecundity data were obtained there as byproducts of a variety of ocher studies con-

ducted between 1986 and 1995. In some uses, I have expanded data sets that were presented earlier, e.g.. Bruce (1990) and Bruce and Hairston (1990). Searches were conducted in the main stream, eight headwater tributaries, and numerous seepages over an elevational range of 730-1 130 m.

The Coweera sites lie within the Coweeta Hydrologic Laboratory, located on the eastern slopes of the Nantahala Mountains, in Macon County, North Carolina. Coweeta is 30 km southwest of Wolf Creek. Sampling at Coweeca was conducted in 1994 and 1995 from 12 sites in the Bali Creek and Shope Fork drainages, whose confluence forms Coweeta Creek. Most salamanders were taken between elevations of 690 m and 1130 m, but a few *D. ocoee* and *D. wrighti* were collected up to 1420 m. Inasmuch as fieldwork at Coweeta was conducted incidental co another project, the samples of gravid females were small, and no deposited clutches were found.

Three species of *Desmognathus* occur at Wolf Creek: the small *D. ocoee*, the midsize *D. monticola*, and the large *D. quadramacuiatus. At Coweeta, the same three species* coexist with the two diminutive species. *D. aeneus* and *D. wrighti.* The former, however, was uncommon at the sampling sites, and neither gravid females nor deposited clutches were observed,

Gravid females were ordinarily identified in the field, returned to the laboratory, anesthetized in MS-222, measured (SVL = snout-vent length in mm), and then preserved in 8% formalin. Yolked follicles in both ovaries were counted (FOL = number of follicles) following dissection. Gravid females were defined as individuals in which the average diameter of ovarian follicles was at least half char of deposited ova. The threshold sizes were 1.5 mm in both *D. wrighti* and *D. ocoee* and 2.0 mm in both *D. monticola* and *D. quadramacuiatus.*

Deposited egg clutches were observed at Wolf Creek only. Some attending females and their clutches were returned to the laboratory where SVLs were measured and eggs were counted. Females and clutches were often held until hatching and then released. Otherwise, females were preserved and dissected to determine the condition of the female reproductive tract immediately after oviposition. In many *D. ocoee,* females were measured and eggs were counted in the field, and the nest was then restored.

The principal statistical test employed was an analysis of covariance of log.-follicle number (ln FOL), with log,-snout-vent length (ln-SVL) as covariate. The ANCOVA design followed Sokal and Rohlf (1995) and was performed with

SYSTAT version 5.2 for Macintosh. Significance was evaluated a: a = 0.05 in all tests.

RESULTS . .

At Wolf Creek, female *D. quadramaculatus* ordinarily attach their eggs to the undersides of large rocks in midstream locations. Those of *D. monticoia* select smaller rocks buried in the streambed or streambank; in some cases, eggs were found attached co several small scones and adjacent roots. The few clutches of *D. monticola* observed at Wolf Creek were all in smaller screams and seepages, whereas chose of *D. quadramaculatus* were in both large and small streams. One clutch of *D. quadramaculatus* and three of *D. monticola* were found in the same small stream within 2 m of one another. The eggs of *D. ocoee* were usually located under moss on soil, logs, and rocks at the edges of streams. Although females of all three species attend their ciutches, in several cases I was unable to locate the females of *D. quadramaculatus* and *D. monticoia.* For these, species identification was verified by raising the eggs to hatching in the laboratory.

Oviposition seasons at Wolf Creek are June in *D. quadramaculatus,* early co mid-July in *D. monticoia,* and mid- co lace July in *D. ocoee.* Egg ciutches of all three species have been found in the field in mid-July.

At Wolf Creek, counts of yolked ovarian follicles in dissected gravid females tended to be higher than the numbers of eggs in field ciutches of all three species (Table 1). This may be the result of several factors, including failure of

TABLE 1. FECUNDITY IN COWEETA AND WOLF CREEK *Desmognathus.*

Locality and species	n	Range	Mean	SD
Ovarian follicles per female				
Coweeta				
D. quadramacuiatus	5	38-69	54.2	11.78
D. monticola	8	2244	29.9	6.99
D. ocoee	12	12-28	17.3	4.39
D. wrighti	4	8-10	9.3	0.96
Wolf Creek				
D. quadramaculatus	13	42-61	52.4	6.06
D. monticola	23	19-39	29.0	5.57
D. ocoee	17	9-22	15.8	3.88
Eggs per deposited clutch				
D. quadramaculatus	3	38–55	45.0	a.89
D. monticola	5	la-27	25.0	3.94
D. ocoee	29	5-23	13.2	3.89

females to deposit their full ovarian comple-
ments, egg mortality after oviposition, as well
as my failure co locate all eggs in a clutch. The
last factor was more of a problem in *D. monticola,*
where eggs were often scattered on several small
rocks in saturated gravel beds. Dissection of fe-
males taken with clutches sometimes revealed
one or a few orange-colored atretic follicles in
the ovaries. Thus females may retain and resorb
some yolked follicles.

To investigate the relationship between body
size and fecundity, I used a power function ap
plied to SVL and FO L (Fig. 1). The power func-
tion is appropriate because SVL is a linear di-
mension and follicle number is expected to vary
according to body volume. A separate analysis
of covariance of ln-FO L, with ln-SVL as covar-
iate, was conducted for each assemblage of spe-
cies (Table 2). Slopes of both regression lines
in Figure 1 were highly significant (Table 2, test
2). In neither analysis was there a significant
interaction between species and ln-SVL (Table
2, test I), thus supporting the assumption of
homogeneity of slope among treatments (spe-
cies). Subsequent analyses of common regres-
sion equations (Table 2, test 3) showed that at
Coweeta there was no significant difference
among species in mean ln-FOL adjusted for
common mean ln-SVL but that at Wolf Creek
the difference was significant. That is, a com-
mon regression line provided an adequate fit
for all four species ac Coweeta but not for the
three Wolf Creek species. Nevertheless, the
combined Wolf Creek data showed a reasonably
close approximation to a common regression
(Fig. 1). The model is considered adequately
descriptive for the purposes of this study, be-
cause the relationship of interest is between age
at first reproduction and mean clutch size.

The common regressions should not obscure
the observation that the correlation between
fecundity and SVL is weak or absent within sev-
eral of the populations sampled (Table 3). One
striking discrepancy in Table 3 is the lack of a
significant correlation of ln-FO L with ln-SVL
in the large sample of brooding females of *D.
ocoee* from Wolf Creek, even though the cor-
relations were significant in the smaller samples
of gravid females of this species at both locali-
ties. The explanation for the poor correlation
of fecundity and body size may derive from the
high residual variance in clutch size combined
with an unusually narrow range of female body
size in desmognachines, as documented for Wolf
Creek (Bruce, 1993) and observed in ocher mul-
tispecies assemblages of desmognathines (Or-
gan, 196 l; Juterbock, 1978).
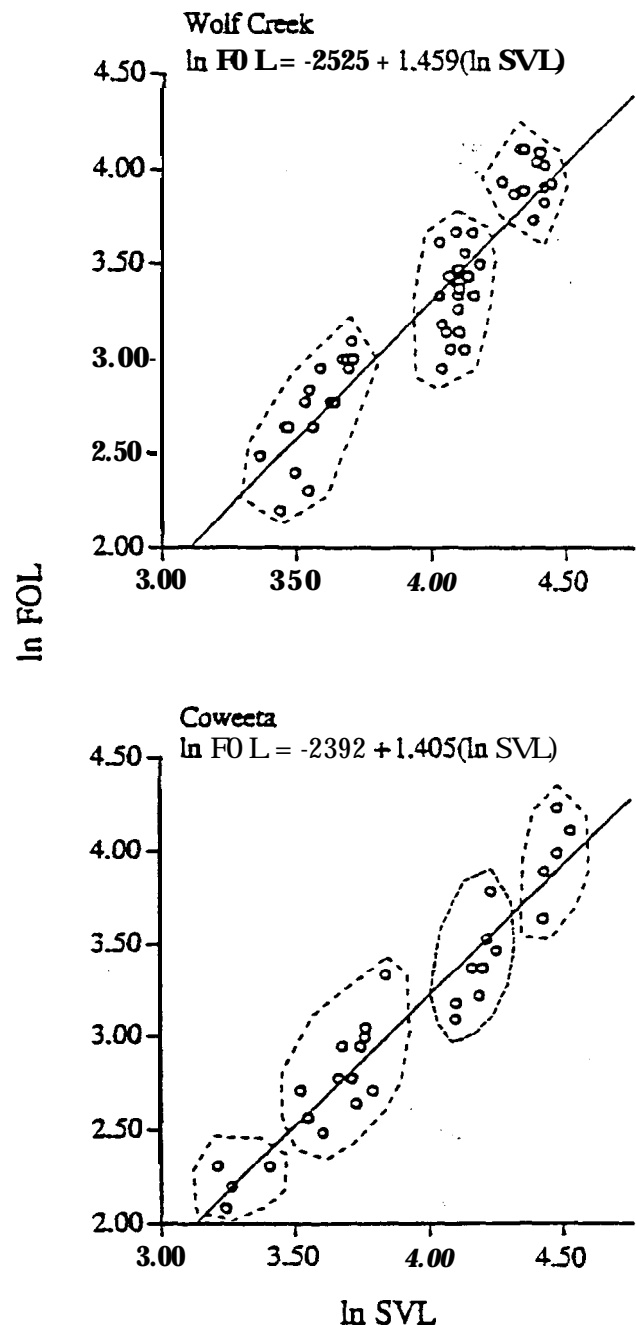
Ages at first reproduction for females at Wolf

Fig. 1. Regressions of follicle number (FOL) on
snout–vent length (SVL) for log.-transformed data
from gravid females of *Desmognathus.* From left to
right the polygons outline clusters of points for *D.
ocoee, D. monticola,* and *D. quadramaculatus* at Wolf
Creek and *D. wrighti, D. ocoee, D. monticola,* and *D.
quadramaculatus* at Coweeta.

Creek are 4–5 yr in *D. ocoee,* 5–7 yr in *D. mon-
ticola,* and 7-S yr in *D. quadramaculatus* (Cas-
tanet et al., 1996). Comparable estimates have
been obtained for the Coweeta populations (J.
Castanet, H. Francillon-Vieillot, R. Bruce, un-
publ.). The estimates suggest that the average
difference is approximately 1 yr between suc-
cessive species in the body-size sequence. How-
ever, the model does not require a 1-yr differ-

TABLE 2. ANALYSIS OF COVARIANCE OF LOG.-FOLLICLE NUMBER (ln-FOL) IN *Desmognathus*. The covariate is log.-snout–vent length (ln-SVL).

Locality	Source of variation	df	MS	F	P
Wolf Creek Within					
	(1) Differences among slopes	2	0.063	2.20	0.122 ns
	Error	47	0.023	.	
	Total				
	(2) Slope of common regression	1	11.342	305.81	< 0.001
	Error	51	0.037		
	(3) Deviations from common intercept among species	2	0.207	6.86	0.002
	Error	49	0.030		
Coweeta	within				
	(1) Differences among slopes	3	0.038	1.42	0.264 ns
	Error	21	0.027		
	Total				
	(2) Slope of common regression	1	8.763	281.75	< 0.001
	Error	27	0.031		
	(3) Deviations from common intercept among species	3	0.055	1.97	0.145 ns
	Error	24	0.028		

ence but only that the difference between successive species is constant.

At Wolf Creek, the ratios of mean ovarian follicle number are 1.81 for *D. quadramaculatus*: *D. monticola* and 1.84 for *D. monticola*: *D. ocoee*. The fecundity ratios based on deposited clutches are similar: 1.80 for *D. quadramaculatus*: *D. monticola* and 1.89 for *D. monticola*: *D. ocoee*. Using the ratios of follicle counts, and assuming uniform survival through life, a 1-yr step in age at first reproduction, and annual reproductive cycles, the mean annual survival rate that would yield equal R_0 is $s = 1/1.81 = 0.552$ in *D. quadramaculatus* and *D. monticola* and $s = 1/1.84 = 0.543$ for *D. monticola* and *D. ocoee*. These are similar to published survival values for *D. ocoee* (Tilley, 1980) and *D. monticola* (Bruce, 1995). Combining the survival estimates with the observed fecundity values, where b/2 = daughters per year, and basing age at first reproduction

on skeletochronological estimates (Castanet et al., 1996), will yield R_0 values that vary around 1.0 in all three species.

Given a constant fecundity ratio, the relationship between fecundity (b) and age at first reproduction (a) is the exponential function, $b = ce^{Ma}$, where M is the instantaneous mortality rate that can be calculated from annual survival, $s = e^{-M}$. Using $k = 1.64$ as a common fecundity multiplier yields $s = 1/k = 0.543$, and $M = 0.610$. If the successive values of a are 5, 6, and 7 yr, then $b = 0.723e^{0.610a}$, approximately, for the Wolf Creek assemblage. The average adult female lifespan can be calculated from $1/M = 1.64$ yr and is identical for the three species under the assumptions of the model.

In the small Coweeta sample, the ovarian follicle ratios are 1.81 for *D. quadramaculatus*: *D. monticola*, 1.73 for *D. monticola*: *D. ocoee*, and 1.86 for *D. ocoee*: *D. wrighti*. Not only are these

TABLE 3. CORRELATION BETWEEN ln-FOL AND ln-SVL IN INDIVIDUAL SAMPLES OF *Desmognathus*. Analysis restricted to those samples where n > 5.

Locality	Sample	n	r	t	P
Wolf Creek	*D. quadramaculatus*, gravid	13	0.016	-0.052	0.960
	D. monticola, gravid	23	0.296	1.418	0.171
	D. ocoee, gravid	17	0.796	5.091	< 0.001
	D. ocoee, brooding	29	0.098	-0.510	0.614
Coweeta	*D. monticola*, gravid	8	0.795	3.206	0.018
	D. ocoee, gravid	12	0.698	3.087	0.012

remarkably uniform, they are very similar to the Wolf Creek ratios. The follicle ratio of the largest to the smallest species at Coweeta, *D. quadramaculatus: D. wrighti*, a three-step sequence, is 5.83, and $5.83^{1/3} = 1.80$, which can be used as the common fecundity multiplier at Coweeta. Substitution of this value in the expressions given above yields estimates of mean annual survival. $s = 0.536$, and instantaneous mortality rate, $M = 0.587$.

DISCUSSION

*Body-size variation_*-Explanations of variation in body size in *Desmognathus* have often been framed in terms of trade-offs in resource allocation among the competing processes of growth, maintenance, storage, and reproduction. Most investigations of this kind have involved *D. ocoee* (Tilley, *1980;* Horn. 1988; Bernardo, 1994). An underlying theme emerging from these studies is that maturation essentially halts growth in females and thereby limits body size and size-related fecundity. Thus, the decision to mature at one age or the next may depend on extrinsic levels of mortality in-the ecosystem in question and the probability of survival to the next year. However, Bernardo (1994) suggested that the difference in age at maturity may derive from differential selection on body size itself or on egg size via correlational selection on body size.

For interspecific variation in body size, the standard explanation derives from Tilley's (1968) conjecture on the role of predation in regulating desmognathine populations, followed by Hairsron's (1986) experimental demonstration of interspecific interactions in a four-species assemblage. The essential evolutionary interpretation. is that allopatric speciation results in some initial body-size variation; reestablishment of contact leads to predation of the larger species on the smaller and, to a lesser degree, competition favoring the former; the smaller species shifts to more terrestrial habitats, which for desmognathines are presumably less satisfactory than the theoretically ancestral aquatic habitats; and the smaller species evolves adaptations co the new habitat_ According to this argument, predation and competition, through their effects on mortality and other demographic attributes, represent the factors responsible for the evolution of the body-size gradient in *Desmognathus* (Hairston, 1986).

This explanation suffers from the absence of reliable survivorship data. Organ's (I96I) survivorship curves and life tables were based on the questionable interpretation that the five species he studied all reproduced initially at the same age. Other survivonhip data deal with single species and are difficult to use comparatively (Danstedt, 1973; Tilley, 1980; Bruce, 1995). Hairston's (1986, 1987) analysis assumed that an evolutionary shift co terrestrial habitats by the smaller species improved survival, but his experiments were not designed co generate survival data for the four species in question. For example, it is not known whether survival of *D. ocoee is* lower than char of the larger *D. monticola* and *D. quadramaculatus* because the former is eaten by the latter two species or higher than that of the larger species because *D. ocoee* has shifted to safer, more terrestrial habitats.

*Demography.-*The fecundity data presented herein, coupled with recent, more reliable data on body size and age at first reproduction (Bruce. 1993; Castanet et al., 1996), suggest that a close linkage or symmetry exists among age at first reproduction, body size, and fecundity in desmognathines. If this relationship is tied to similar survival probabilities among species, then a fixed relationship among life-history variables ma7 prescribe the direction of evolutionary transformations under a variety of selective regimes. Because of geographic variation in body size and fecundity, the paaem may not be as evident in studies where data from different populations have been pooled (e.g.. Tilley, 1968). The valuable table of desmognathine life-history data provided by Tilley and Bernardo (1993) summarizes fecundity for a wide range of species and populations but does not permit evaluation of Symmetry relationships in particular assemblages. If external mortality drives the evolution of life histories (Stearns, 1992; Chamov, 1993), and if mortality varies geographically, then it is at the local level that symmetry will be detected.

The demographic argument offered herein assumes uniform size-specific survivorship and fecundity schedules across species boundaries. The theoretical basis of the argument is the observation of relative morphological uniformity among desmognathines (Sweet, 1973, 1980). This leads to the proposition that morphological uniformity has prescribed a common set of intrinsic survival and fecundity schedules. Adjustments in body size, evolved in response to various environmental factors, and accomplished by shifts in age at first reproduction. provide access to these schedules. The object of selection is body size; because of the invariance in demographic parameters, a change in size can be attained without a cost in fitness through change in age at first reproduction.

There are several difficulties with the model. One involves egg size and hatchling size. Variation in egg size influences larval growth and metamorphosis in salamanders (Kaplan, 1980. 1985). The present model treats individual eggs as equivalent across species, whereas in reality they vary in size. Thus a comparison of egg number does not precisely reflect differences in reproductive allocation, inasmuch as clutch volume is a product of egg volume and number.

Second. rigorous application of the model requires that pre- and posunaturational survival each be constant and equal among species of a given assemblage. This is unlikely. Nevertheless, the basic argument does not require demographic identity, just a high degree of similarity.

Selective factors.-If the principal object of selection in *Desmognathus* is body size. then what are the selective factors? The traditional explanation is that the ranges of body sizes and life histories are products of smaller species being ousted from favored aquatic habitats by unfavorable demographic environments that derive from interactions with larger congeners (Hairston, 1986). My extension of this model is based on the premise that morphologically similar species share a common set of responses to the opportunities afforded by the resource gradient of Appalachian ecosystems. The evolution of body size is seen as an active process driven by positive selection in response to unexploited resources of a rich environment.

Resource variables that surely have contributed to the diversification of desmognathines are the composition of the substratum and substratum particle size. Schwenk and Wake's (1993) functional-morphologic analysis showed that several of the skeletomuscular synapomorphies of desmognathines are adaptations to head-first burrowing involving crevice widening through dorsoventral wedging of the head. I suggest that larger species are adapted co the large rocks found within the stream boundary; middle-size species to the smaller rocks and gravel of the streambank; and smaller species to wood, leaves, and moss of the forest floor. Several experiments on habitat choice in a variety of desmognathines have demonstrated these relationships (Krzysik and Miller, 1979; Carr and: Taylor, 1985; Southerland, 1986).

Further *resolution and summary.*—Some assemblages of desmognathines contain two or more species of similar body size and life history. Such ecological analogues are usually found in ecosystems where precipitation is high and the

moisture gradient is particularly wide. One example is *D. marmoratus* and *D. quadramaculatus*, which coexist in numerous watersheds, with the latter being somewhat more terrestrial. *Desmognathus monticola* and *D. fuscus* coexist at some localities, particularly in the central Appalachians where the larger aquatic forms are absent (e.g., Krzysik, 1979). In the Great Smoky Mountains, there are complex patterns of ecological overlap of the similar-sized *D. imitator, D. acoee,* and *D. santeetlah* (Tilley, 198 1). The two terrestrial species, *D. aeneus* and *D. wrighti,* coexist in the southern Nantahala Mountains, representing the most mesic ecosystem in the Appalachians (Bruce, 199 1). If the occurrence of ecological analogues is explainable on the basis of the breadth and richness of the resource base, their coexistence in no way invalidates the model of adaptive radiation presented herein.

Invariant relationships among age at first reproduction, adult body size, fecundity, and survival in desmognathines would represent life-history symmetry (Charnov, 1993). Unlike most instances of symmetry, where the underlying cause is unknown, the causal factor in desmognathines may be the morphological constraint imposed by the unique set of feeding/burrowing synapomorphies. A test of the model will require a more intensive investigation of life histories in an expanded set of assemblages encompassing a greater variety of species than occurs at Wolf *Creek* and Coweera.

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