HERPETOLOGICAL MONOGRAPHS

COMMUNITY ASSEMBLY IN THE SALAMANDER GENUS DESMOGNATHUS

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ABSTRACT: In this paper, I present a model of community assembly in the salamander genus Desmognathus based on a survey of assemblage composition throughout the range of the genus. The 21 species of Desmognathus can be sorted into three life-history categories, namely, stream, streamside, and forest, based on duration of the larval phase and a suite of other life-history and morphological traits that are correlated with habitat use of the several life-history stages. In most assemblages having all three life-history categories, stream species are larger than streamside species, and the latter species are larger than forest species. An evaluation of the literature on interspecific competition and predation (i.e., intraguild predation) in Desmognathus indicates that these processes are important in structuring assemblages of these salamanders. Thus, niche assembly, as opposed to dispersal assembly (i.e., neutral model), seems to be a valid model of community assembly in Desmognathus. Only streamside species occur throughout the range of the genus, and these forms alone are found around the periphery of the range. One to three streamside species form the base of extant assemblages of Desmognathus, with stream and forest species contributing to the more diverse assemblages of the southern Appalachian region. The maximum numbers are two or three streamside species, two or three stream species, and two forest species, although assemblages of more than six species are undocumented. I suggest that the rapid evolutionary diversification in body size and life history in Desmognathus that has generated the complex assemblages of this genus in the Appalachians has been facilitated by a high level of life-history symmetry in these salamanders.

Key words: Body size; Interspecific competition; Intraguild predation; Life history; Niche assembly; Salamander

The origin of diversity in ecological communities has been viewed from two principal perspectives, known as niche assembly and dispersal assembly or neutral theory (Hubbell, 2001). Under the former perspective, interspecific competition and other interactions, such as intraguild predation (IGP), are viewed as processes that provide community structure, limit community membership, and thereby engender “rules” that regulate the assembly and composition of such communities and lead to stable equilibria (Gotelli and McCabe, 2002). The classic application of this concept is Diamond’s (1975) analysis of the avian communities of the Bismarck Islands. Strong arguments for niche assembly have been made for other communities, e.g., desert rodents (Brown et al., 2000, 2002) and Galápagos finches (Grant and Grant, 2006, 2008). In contrast, dispersal assembly posits that communities are essentially random assemblages of species originating through processes of dispersal and extinction that have strong stochastic elements, as represented in MacArthur and Wilson’s (1967) theory of island biogeography. Hubbell (2001) provided an extension of the MacArthur and Wilson model that incorporated the speciation process and elements of both niche assembly and dispersal assembly into a “unified neutral theory.” Tilman (2004), Gravel et al. (2006), and Scheffer and van Nes (2006) have extended the analysis in attempts to resolve differences between the two theories. A recent review of the literature on the neutral theory was provided by Beeravolu et al. (2009).

Assemblages of plethodontid salamanders in eastern North America are often rich in species and may include up to five or six species of a given genus. Interspecific competition and predation are presumed to play important roles in structuring these assemblages (Bruce, 2007, 2008; Hairston, 1996; Wells, 2007). One such genus is Plethodon, comprising 45 species in eastern North America. Adams’s (2007) study of community assembly in Plethodon indicated that assemblages (maximum five species) were nonrandom, stable, and competition based.
The 21 species of *Desmognathus* currently recognized occur in the eastern United States and extreme southeastern Canada, with maximum species richness in the southern Appalachian Mountains. The genus illustrates the classic features of an adaptive radiation, i.e., “a burst of speciation and rapid phenotypic evolution under conditions of high ecological opportunity” (Schluter, 1998). In the genus *Desmognathus*, such a burst of speciation and lineage diversification began approximately 20 million yr ago (Kozak et al., 2005). Diversity at the species level in *Desmognathus* may be much greater than recognized by current taxonomy, according to recent phylogenetic assessments by Kozak et al. (2005), Jones et al. (2006), and Beamer and Lamb (2008). Examples are the identification in several species of independent lineages that have allopatric or parapatric distributions (Beamer and Lamb, 2008; Kozak et al., 2005). Another example is the complex relationship of *D. quadramaculatus* and *D. marmoratus* throughout the range of the latter species (Jones et al., 2006). However, the splitting and naming of lineages that are now included under a single species name may not change our understanding of assemblage organization, because species richness and ecological structure in most assemblages will be unaffected.

Of great interest in *Desmognathus* is the correlation among body size, other morphological traits, life history, and habitat use—very simply, the larger species are more aquatic and the smaller species are more terrestrial. The correlation holds, with some exceptions, no matter which species occur in a particular assemblage. It provides a basis for sorting the species into three life-history categories that I refer to as stream, streamside, and forest. Stream species (n = 4) tend to be large, occur mainly in the stream and on the stream bank, and have a larval phase that extends for ≥2 yr. Streamside species (n = 14) are usually intermediate in size, live on the stream bank and adjacent forest, and have a relatively brief larval phase of ≤1 yr. Forest species (n = 3) are tiny; lack a free-living larval stage (i.e., show direct development); and live under logs, leaf litter, and moss on the forest floor. Although there is overlap in adult body size and habitat use of the species, the life-history criterion serves to separate the species into three discrete categories. Variation among the species in larval period is shown in Table 1.

The habitat use function in *Desmognathus* may be formulated according to the distribution of individuals along the aquatic to terrestrial habitat gradient, i.e., the frequency distribution of distances of individuals of a given species from the stream (see Hairston, 1987: Fig. 6.1; Petranka and Smith, 2005: Fig. 3). The distribution will vary geographically and temporally, and locally with topography, but it should be informative for interspecific comparisons at a given time and place. Although the correlation of body size with habitat use in *Desmognathus* is well documented (e.g., Hairston, 1949; Krzysik, 1979; Organ, 1961b; Petranka and Smith, 2005), there is considerable overlap in habitat use. For example, the three smallest and most terrestrial species, *D. aeneus*, *D. organi*, and *D. wrighti*, often occur in wet sites in proximity to larger species. *Desmognathus wrighti* have been recorded in the winter among rock and gravel in the saturated banks of seepages (Bruce, 1977). Such habitats are selected for oviposition and nesting by females of the closely related *D. organi* in late summer (Organ, 1961a). *Desmognathus aeneus* occurs in seepage areas, often in damp moss, and such habitats frequently serve as nesting sites (Harrison, 1967), although females also may select nesting sites in the forest some distances from seeps and streams (Jones, 1981). In the southern Nantahala Mountains, both *D. aeneus* and *D. wrighti* occur frequently in moss and leaf litter close to the margins of streams (Hining and Bruce, 2005). A common associate of both species is *D. ocoee*. In these same watersheds, I have occasionally observed the large stream species *D. quadramaculatus* under logs in the forest, 5–10 m from the stream edge. Juveniles and adults of *D. quadramaculatus*, like others in the genus, have a terrestrial feeding mechanism involving tongue protrusion (Deban and Marks, 2002), and they feed largely on terrestrial prey (Davic, 1991; Martof and Scott, 1957). The large streamside species *D. monticola* is even more frequently found in forest floor habitats. Although the most aquatic species,
D. marmoratus, also has a terrestrial feeding apparatus (Deban and Marks, 2002), its prey are largely aquatic (Martof and Scott, 1957); it seems that individuals seldom forage beyond the stream edge and seldom interact with the terrestrial species or with the more terrestrial of the streamside species. However, there may be indirect interactions if the degree of terrestrialism of D. quadramaculatus is affected by the presence or absence of D. marmoratus in a watershed.

Populations of some smaller species of Desmognathus undergo niche contraction or expansion along the habitat use dimension depending on the presence or absence of larger congeners. For example, the streamside species D. monticola and D. fuscus may shift to more terrestrial habitats in the presence of the predatory aquatic species D. quadramaculatus (Fauth, 1998; Grover, 2000; Rissler et al., 2004; Southerland, 1986b,d), and D. fuscus in response to D. monticola (Southerland, 1986b), although the evidence is contradictory for the response of D. monticola to D. quadramaculatus (cf. Grover, 2000; Rissler et al., 2004). However, such shifts do not affect life-history status, if the principal criterion is the duration of the larval period.

Subdividing Desmognathus into life-history categories serves a useful purpose for evaluating assemblage structure, but it tends to obscure the similarities among species that distinguish this genus from other plethodontids (Schwenk and Wake, 1993). If life histories of organisms are constrained by trade-offs among traits that act directly or indirectly on fitness, then in a morphologically conservative genus such as Desmognathus such conservatism may be paralleled by conservatism in life-history constraints. Thus, the extreme variation observed in life history in the genus may reflect selection within a common suite of trade-off relationships, as populations and species exploited opportunities along the aquatic-to-terrestrial habitat gradient. Constraints are expressed in trade-offs in propagule size, growth rate, age at first reproduction, adult body size, fecundity, and survival that have been reported in some assemblages but need to be further investigated in these and other assemblages. Specifically, primary traits that vary markedly,

<table>
<thead>
<tr>
<th>Species</th>
<th>Life-history category</th>
<th>Larval period (mo)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>D. quadramaculatus</td>
<td>1</td>
<td>24–48</td>
<td>Camp et al., 2000; Bruce, 1988; Organ, 1961b</td>
</tr>
<tr>
<td>D. folkertsi</td>
<td>1</td>
<td>24</td>
<td>Camp et al., 2002</td>
</tr>
<tr>
<td>D. marmoratus</td>
<td>1</td>
<td>10–20, 36</td>
<td>Bruce, 1985; Martof, 1962</td>
</tr>
<tr>
<td>D. walteri</td>
<td>1</td>
<td>20–24</td>
<td>Juterbock, 1984</td>
</tr>
<tr>
<td>D. abditus</td>
<td>2</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>D. auriculatus</td>
<td>2</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>D. breviloquorum</td>
<td>2</td>
<td>12</td>
<td>Means, 1974; Trauth et al., 1990</td>
</tr>
<tr>
<td>D. carolinensis</td>
<td>2</td>
<td>2–8</td>
<td>Tilley, 1973</td>
</tr>
<tr>
<td>D. conanti</td>
<td>2</td>
<td>≤13</td>
<td>Jones, 1986; Mount, 1975</td>
</tr>
<tr>
<td>D. fuscus</td>
<td>2</td>
<td>8–14</td>
<td>Danstedt, 1975; Organ, 1961b; Wilder, 1913</td>
</tr>
<tr>
<td>D. unitor</td>
<td>2</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>D. monticola</td>
<td>2</td>
<td>8–13</td>
<td>Bruce, 1989; Juterbock, 1984; Organ, 1961b</td>
</tr>
<tr>
<td>D. ochrophaeus</td>
<td>2</td>
<td>≥8–10</td>
<td>Bishop, 1941</td>
</tr>
<tr>
<td>D. ocoee</td>
<td>2</td>
<td>9–10</td>
<td>Bernardo and Agosta, 2003; Bruce, 1989; Huheey and Brandon, 1973</td>
</tr>
<tr>
<td>D. orestes</td>
<td>2</td>
<td>8–9</td>
<td>Organ, 1961b</td>
</tr>
<tr>
<td>D. planiceps</td>
<td>2</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>D. sauteedh</td>
<td>2</td>
<td>&lt;12</td>
<td>Jones, 1986</td>
</tr>
<tr>
<td>D. aeneus</td>
<td>3</td>
<td>0</td>
<td>Harrison, 1967</td>
</tr>
<tr>
<td>D. organi</td>
<td>3</td>
<td>0</td>
<td>Organ, 1961a,b</td>
</tr>
<tr>
<td>D. wrighti</td>
<td>3</td>
<td>0</td>
<td>Hining and Bruce, 2005</td>
</tr>
</tbody>
</table>

1 Where data on larval phases are lacking, I have assigned species to categories based on life-history traits of their closest relatives.
2 Major sources of data on larval periods are listed.
including propagule size, age and size at metamorphosis, age and size at first reproduction, and fecundity (Bruce, 2005: Table 1; Tilley and Bernardo, 1993: Table 1), do so within a framework of apparent invariance in several relationships between life history and demographic elements. Invariant relationships that suggest themselves include intrinsic larval and juvenile growth rates (Bruce, 1996, 2010); the regression of fecundity on female age and size (Bruce, 1996; Tilley, 1968); the ratio of clutch volume to body volume (Salthe, 1969); the ratio of propagule size to adult size (Beachy, 1993; Tilley and Bernardo, 1993); the relationship among body size, fecundity, and survivorship (Bruce, 1996); and aspects of sexual size dimorphism (see Variation in Body Size below). As a working hypothesis, and limiting case, I propose that niche differentiation in *Desmognathus* follows scaling laws incorporating life-history trade-offs that covary predictably and are common to all species. Such trade-offs reflect the morphological conservatism of the genus (Sweet, 1973, 1980) and the unique adaptations for feeding and burrowing (i.e., synapomorphies) of the constituent species (Schwenk and Wake, 1993).

A phylogenetic assessment of molecular and morphological variation in *Desmognathus* by Kozak et al. (2005) provided a basis for formulating assembly rules that generate community structure in the genus. Kozak et al. (2005) hypothesized that the adaptive radiation of the genus began with a direct-developing ancestor, followed by an early phase of ecomorphological divergence (i.e., in body size particularly, and correlated life-history traits) of geographically overlapping lineages, under the selective influence of strong ecological interactions (i.e., interspecific competition, IGP) in favorable environments (i.e., moist forests) of the Appalachian Mountains. This radiation led to the buildup of stable assemblages of stream-, streamside-, seepage-, and forest-adapted species. Presumably, the early stages of the process would involve contact of reproductively isolated populations in which some size differences had evolved before contact, followed by selection for additional niche differentiation elicited by species’ interactions in sympathy, eventually generating the aquatic to terrestrial sequences of species seen in extant assemblages. This model is similar to that suggested by Tilley (1968). Although the Tilley (1968) model derived from the hypothesis that the large, aquatic species were ancestral and that selection on the smaller member of an interacting pair generated even smaller, more terrestrial species under the influence of IGP, Tilley’s basic premise can be accommodated within the Kozak et al. (2005) model.

The later stage (or perhaps parallel stage) of *Desmognathus* evolution, according to Kozak et al. (2005), involved the splitting of geographically isolated and ecomorphologically similar sets of populations into separate, similar species, having allopatric or parapatric distributions, as in the various lineages of *D. conanti*, *D. auriculatus*, and *D. ocoee* identified by these authors and Beamer and Lamb (2008). The recognition of *D. ochrophaeus* as a complex of five parapatric/allopatric species by Anderson and Tilley (2003) and Tilley and Mahoney (1996) and *D.wrighti* as a two-species complex by Crespi et al. (2010) are other examples. This process generates additional species but does not affect structure and richness within assemblages. Physical-environmental factors contributing to the speciation process include historical climatological variation associated with mountain topography and shifts in drainage patterns (Crespi et al., 2003; Jones et al., 2006; Kozak and Wiens, 2006; Tilley and Mahoney, 1996; Voss et al., 1995).

One approach in evaluating community assembly is to generate pseudocommunities randomly from the available species pool of the taxon in question and to compare these null-model communities with actual, observed communities. Statistical deviation in composition of the actual communities from those of the randomly assembled null communities is considered evidence that the real communities are products of a competition-based, niche assembly process (e.g., Gotelli and McCabe, 2002). Problems with this approach arise when some species are narrowly distributed and widely separated from others and thus unlikely to coexist. Adams (2007) addressed this problem in the genus *Plethodon* by subdividing the overall source pool of eastern *Plethodon* into 14 regional pools and
assigning each real assemblage to one of the regional pools. He then compared randomly derived assemblages from each regional pool with actual assemblages in that region. In evaluating results, Adams (2007) used the criterion of evenness, under which species are added from different functional groups or guilds before additional species from the same guild are added (Brown et al., 2002; Fox, 1987). Adams (2007) found that *Plethodon* assemblages were nonrandom, with a high degree of evenness, in accordance with the competition model. In *Desmognathus*, where the total source pool is smaller and much of the range of the genus is occupied by a single species, subdividing the source pool would still result in low probabilities of certain combinations because of geography and the generally low dispersal abilities of *Desmognathus*.

My approach herein is to begin with a review of interspecific variation in body size in *Desmognathus*, based largely on studies that have compared size in two or more sympatric species. I then present a database of *Desmognathus* assemblages over the range of the genus and examine it for patterns of representation of life-history categories. I follow this with a more critical review of interspecific interactions in the genus than has heretofore been conducted (Bruce, 2007, 2008; Hairston, 1996; Wells, 2007). I then provide an assessment of community assembly in *Desmognathus*, under the niche assembly model, and I pose the following questions: (1) Across the range of the genus, do increases in species number follow a stepwise process, such that the sequence of addition of species provides evenness in representation of life-history categories? (2) Does the observed pattern allow for the prescription of assembly rules? (3) What factors have most likely contributed to the observed variation in assembly composition? Finally, I offer suggestions on the role of life-history constraints within and among species in the evolutionary history of *Desmognathus*.

A Note on Terminology

I have referred earlier to a set of *Desmognathus* species occupying a given area (e.g., a small watershed; see *Interior* (Appalachian) Assemblages below) as an assemblage, following the use of Fauth et al. (1996) who defined an assemblage as the members of a given taxon (in the present case a genus) living in the same community. In *Desmognathus*, it is unlikely that the extreme forms on the habitat use gradient, i.e., the aquatic *D. marmoratus* and the terrestrial *D. aeneus, D. organi*, and *D. wrighti*, should be considered members of the same guild; otherwise, the term ensemble would be preferred over assemblage (Fauth et al., 1996). Nevertheless, in essentially every assemblage of *Desmognathus*, adjacent pairs of species on the aquatic-to-terrestrial habitat gradient overlap considerably in resource use (e.g., food, cover objects); thus, effects on interspecific interactions that result from the loss or gain of a species at either end of the habitat continuum may have cascading effects throughout the assemblage. Although the species of *Desmognathus* are not herein considered members of a single guild, I do use the label IGP in referring to predation of one species of *Desmognathus* on another, because of the currency of this term in the literature (e.g., Rosenheim, 2007).

Materials and Methods

Although this paper is primarily a literature review, I have incorporated older (1985–1995) unpublished data from one locality (Wolf Creek) in the Cowee Mountains and recent data (2006–2010) from two areas of the southern Nantahala Mountains, all in North Carolina, into the database on variation in body size presented herein. The Wolf Creek watershed lies on the west slope of Cullowhee Mountain, a spur of the Cowee Mountains, in Jackson County. Localities in the southern Nantahala Mountains include tributary watersheds in the Coweeta Creek watershed at Coweeta Hydrologic Laboratory, and several tributary watersheds of the upper Nantahala River, including the Park Creek, Little Rock Branch, and Kimsey Creek watersheds, all in Macon County. Measurements of standard length (SL) were taken from the tip of the snout to the posterior end of the cloacal slit to the nearest 0.1 mm on living salamanders anesthetized in a solution of the anesthetic tricaine methanesulfonate (MS-222). Individuals of the larger species (*D. quadramaculatus, D. monticola, D. ocoee*) were then fixed in 10% formalin and later transferred to 70%

2011] HERPETOLOGICAL MONOGRAPHS 5
ethyl alcohol; the reproductive organs were examined by dissection, and the sex and reproductive status were determined. For the smaller species (D. aeneus, D. wrighti), the body cavity of living, anesthetized individuals was examined by fiber-optics illumination with a dissecting microscope, and sex and reproductive status were determined. Most of these individuals were subsequently released at the sites where they had been captured.

Criteria for distinguishing immature and mature individuals of either sex followed Bruce (1993), except, as in Bruce et al. (2002), I scored all females as mature if vitellogenesis had been initiated. This scoring required incorporation of the measurements of most females scored as submature in the earlier studies of Wolf Creek (Bruce, 1993; Castanet et al., 1996) into the database of mature females.

VARIATION IN BODY SIZE

The correlation between body size and habitat use in Desmognathus involves other morphological traits, such as tail shape, but overall Desmognathus is a morphologically conservative genus (Sweet 1973, 1980). Comparative body size data compiled from the literature and including 15 of the 21 species are summarized in Table 2. In those comparisons involving species of different life-history categories, the ranking of large to small is stream species > streamside species > forest species. Exceptions to the trend are considered under Assemblage Structure.

Table 2.—Comparative body sizes of adult Desmognathus based on published data. The list is restricted to studies comparing two or more species.

<table>
<thead>
<tr>
<th>Species (life-history category)</th>
<th>Size rank</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>fuscus (2) &gt; ochrophaeus (2)</td>
<td></td>
<td>Bishop, 1941</td>
</tr>
<tr>
<td>quadramaculatus (1) &gt; monticola (2) &gt; ocoee (2)</td>
<td></td>
<td>Bruce, 1993; Bruce et al., 2002; Castanet et al., 1996</td>
</tr>
<tr>
<td>quadramaculatus (1) &gt; folkertsi (1)</td>
<td></td>
<td>Camp et al., 2002; Camp and Marshall, 2006</td>
</tr>
<tr>
<td>conanti (2) &gt; santeetlah (2)</td>
<td></td>
<td>Jones, 1986</td>
</tr>
<tr>
<td>conanti (2) &gt; aeneus (1)</td>
<td></td>
<td>Rubenstein, 1969</td>
</tr>
<tr>
<td>ocoee (2) &gt; aeneus (3) = wrighti (3)</td>
<td></td>
<td>Bruce, 2009; Hining and Bruce, 2005</td>
</tr>
<tr>
<td>weteri (1) &gt; monticola (2) &gt; fuscus (2)</td>
<td></td>
<td>Juterbock, 1978</td>
</tr>
<tr>
<td>monticola (2) &gt; fuscus (2) &gt; ochrophaeus (2)</td>
<td></td>
<td>Krzysik, 1979; Krzysik and Miller, 1979</td>
</tr>
<tr>
<td>monticola (2) = fuscus (2)</td>
<td></td>
<td>Grant et al., 2005</td>
</tr>
<tr>
<td>brindegorum (2) &gt; auriculatus (2) &gt; conanti (2)</td>
<td></td>
<td>Dodd, 1998; Means, 1974</td>
</tr>
<tr>
<td>quadramaculatus (1) &gt; monticola (2) &gt; fuscus (2) &gt;</td>
<td></td>
<td>Organ, 1961b</td>
</tr>
<tr>
<td>onestes (2) &gt; organi (3)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

I have summarized body-size data from my own studies of life histories of Desmognathus in assemblages in the Cowee and Nantahala mountains in Table 3. The table does not include data on D. marmoratus, a species that occurs in the Nantahala River watershed in assemblages in tributary watersheds that support five other species. In small samples (n = 16) of this species taken in 1992–1993, living individuals were measured for standard length but were not sexed. Maximum size was 85 mm SL. Thus, this species, the most aquatic in the genus, seems to rank between D. quadramaculatus and D. monticola in body size in the Nantahala assemblages. Martof (1962) reported maximum body lengths of 77 mm (males) and 78 mm (females) in northern Georgia populations. However, his measurements were taken to the anterior angle of the vent on formalin-preserved specimens. These individuals were probably 85–86 mm SL when alive.

A general trend in Desmognathus is that males reach adulthood at younger ages and smaller sizes than females, and, in most species, males grow to larger sizes. An exception to the latter trend is seen in the smallest species, D. aeneus, D. organi, and D. wrighti, in which males and females attain similar maximum sizes. The trends are evident in many of the studies cited in Table 2 and in the data presented in Table 3. In all species for which data are available, variances in adult body size, as measured by the standard deviations of SL, are greater in males than in females. In the Cowee and Nantahala samples
Table 3.—Body sizes of adult Desmognathus in assemblages in the Cowee and Nantahala Mountains, North Carolina. For comments on D. marmoratus, see text.

<table>
<thead>
<tr>
<th>Mountain range, watershed</th>
<th>Species, life-history category</th>
<th>Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>SL (mm)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>n</td>
<td>Range</td>
</tr>
<tr>
<td>Cowee</td>
<td>D. quadramaculatus, 1</td>
<td>47</td>
<td>61–100</td>
</tr>
<tr>
<td></td>
<td>D. monticola, 2</td>
<td>99</td>
<td>47–74</td>
</tr>
<tr>
<td></td>
<td>D. ocoee, 2</td>
<td>67</td>
<td>28–51</td>
</tr>
<tr>
<td>Nantahala</td>
<td>D. quadramaculatus, 1</td>
<td>14</td>
<td>74–107</td>
</tr>
<tr>
<td></td>
<td>D. monticola, 2</td>
<td>34</td>
<td>46–77</td>
</tr>
<tr>
<td></td>
<td>D. monticola, 2</td>
<td>76</td>
<td>48–80</td>
</tr>
<tr>
<td></td>
<td>D. ocoee, 2</td>
<td>43</td>
<td>28–50</td>
</tr>
<tr>
<td></td>
<td>D. aeneus, 3</td>
<td>13</td>
<td>18–29</td>
</tr>
<tr>
<td></td>
<td>D. wrighti, 3</td>
<td>12</td>
<td>19–27</td>
</tr>
<tr>
<td></td>
<td>D. ocoee, 2</td>
<td>72</td>
<td>29–53</td>
</tr>
<tr>
<td></td>
<td>D. aeneus, 3</td>
<td>24</td>
<td>16–27</td>
</tr>
<tr>
<td></td>
<td>D. aeneus, 3</td>
<td>17</td>
<td>17–29</td>
</tr>
<tr>
<td></td>
<td>D. wrighti, 5</td>
<td>31</td>
<td>16–26</td>
</tr>
</tbody>
</table>
(Table 3), in correcting for differences in size among species (and considering small numbers in some samples), the coefficients of variation in SL show a remarkable uniformity among species, both within and between sexes.

The limited variation in SL in adult females probably reflects a greater shift in females than males in the allocation of resources from growth and maintenance to reproduction upon sexual maturation (Hom, 1988). This shift may be more pronounced in *Desmognathus* than in other plethodontid salamanders, where females, although older and larger at maturation, grow to equivalent or larger sizes than males (Bruce, 2000).

**Assemblage Structure**

**Peripheral Species and Assemblages**

Toward the northern limit of the range, *Desmognathus* communities contain one or two streamside species, *D. fuscus* only in southeastern Canada and New England, as in New Hampshire (Burton, 1976) and western Massachusetts (Wilder, 1913), or the larger *D. fuscus* and the smaller *D. ochrophaeus*, species that are syntopic in parts of New York (Bishop, 1923, 1941). *Desmognathus fuscus* only is found at the western edge of the range of the genus in Ohio. However, in northeastern Ohio *D. fuscus* occurs in syntopy with *D. ochrophaeus* (Holomuzki, 1980; Pfingsten and Downs, 1989).

In Pennsylvania, a third streamside species, the larger and more aquatic *D. monticola*, may occur in syntopy with *D. fuscus* and *D. ochrophaeus* (Davic, 1953; Krzysik, 1979; Krzysik and Miller, 1979). As shown by Krzysik (1979), there is a correlation between adult body size and the habitat use function in this series. Further south, in Maryland, Danstedt (1975) studied the life history and demography of *D. fuscus* in populations where it occurs by itself in the Piedmont and Blue Ridge, as well as populations where it is syntopic with *D. ochrophaeus* and *D. monticola* further west in the Ridge and Valley Province.

*Desmognathus brinleyorum* occupies part of the western limit of the range of the genus in the Ouachita Mountains of Arkansas and southeastern Oklahoma. As documented by Means (1974, 1999b), it is large for a streamside species, but I consider it a streamside form, based on incomplete evidence for an approximate 1-yr larval period (Trauth et al., 1990). To the south, its distribution borders those of the streamside *D. conanti* and *D. auriculatus*, with the latter species extending to the southwestern limit of the range of the genus in Texas (Means, 1999a). There is apparent syntopy of *D. conanti* and *D. auriculatus* in parts of the western Gulf Coast (Dundee and Rossman, 1989).

Four species of *Desmognathus* occur in Florida: *D. apalachicolae, D. auriculatus, D. conanti,* and *D. monticola*. All species are streamside forms, intermediate in body size and life history. *Desmognathus apalachicolae* and *D. conanti* seem to have parapatric distributions; where either of these species overlaps with *D. auriculatus* in small watersheds, the species segregate into headwater and higher-order streams, respectively (Means, 1975; Means and Karlin, 1989). However, *D. conanti* and *D. monticola* are apparently syntopic within the limited range of the latter in extreme western Florida (Means and Longden, 1970). Only *D. auriculatus* occurs in peninsular Florida, where Dodd (1998) provided habitat and body size data on a population now believed to be extirpated.

Karlin et al. (1984) sampled populations of Northern (*D. fuscus*) and Spotted (*D. conanti*) Dusky Salamanders (all previously within *D. fuscus*) that were each syntopic with none, one, two, and three congeners, according to the 1984 taxonomy of the genus. Populations not syntopic with other *Desmognathus*, and occurring near the periphery of the range of the genus, showed higher levels of heterozygosity than those syntopic with other members of the genus. They interpreted the results as an effect of compression of niche breadth as a consequence of interspecific competition and IGP. Taxonomic changes, including the recognition of additional species since 1984, do not change the overall trend of the Karlin et al. (1984) analysis.

The molecular phylogenetics of Atlantic and Gulf Coastal Plain *Desmognathus* has recently been evaluated by Beamer and Lamb...
(2008), who discovered eight independent lineages among populations originally assigned to three species (D. apalachicolae, D. auriculatus, D. conanti). However, they did not assign new names to the lineages. Moreover, they did not report syntopy between or among any of the lineages; thus, most local “assemblages” throughout the region seem to consist of a single streamside species.

In summary, around the periphery of the range of the genus, the Desmognathus community usually consists of one streamside species. Toward the interior of their ranges, some of these species, especially D. fuscus and D. conanti, exist in syntopy with one or two other streamside species and with species of other life-history categories. Other peripheral species, however, have essentially allopatric or parapatric distributions throughout their ranges (e.g., D. auriculatus, D. brinleyorum). Thus, the widespread occurrence and dominance in species number of streamside species suggests an important role for them in the early history and diversification of the genus.

Interior (Appalachian) Assemblages

In considering the composition of Desmognathus assemblages, the question arises as to the scale of the habitat unit that defines the boundaries of an assemblage. In examining my own data on Desmognathus in the southern Blue Ridge and adjacent Piedmont, I have restricted the analyses to forested watersheds that are drained by second- or third-order streams and their tributaries and that provide a habitat gradient allowing direct or indirect interaction among all the species of Desmognathus found therein.

The most thorough early study of assemblage structure in Desmognathus (and other plethodontids) was Hairston’s (1949) investigation of habitat use in several assemblages in the southern Blue Ridge of western North Carolina and adjacent areas of South Carolina and Georgia. Hairston conducted vertical and horizontal transects in several mountain ranges; the most thorough data were obtained from watersheds in the Black Mountains (Mt. Mitchell and vicinity) of North Carolina that support five desmognathans, now assigned to the species D. marmoratus, D. quadramaculatus, D. monticola, D. carolinensis, and D. organi. The horizontal transects clearly demonstrated the aquatic to terrestrial habitat preferences of these five species in the order listed. In the vertical transects, D. marmoratus and D. monticola were restricted to lower elevations (<915 and <1040 m, respectively), whereas D. organi was generally found at higher elevations (>1050 m). Most areas along the vertical transects supported three species only, and at the highest elevations D. carolinensis and D. organi only were found.

Hairston’s student James Organ (1961b) recorded vertical and horizontal distributions of five species of Desmognathus (in current taxonomy D. quadramaculatus, D. monticola, D. fuscus, D. orestes, D. organi) in the Mount Rogers-Whitetop area of southwestern Virginia. Desmognathus marmoratus (then assigned to the genus Leurognathus) also occurs in the area but was not included in the study. Organ documented the distribution of the five species on six vertical transects taken along streams and roads on different aspects of the mountains. The data showed limited overlap of all five species on any one transect; however, five of the six transects included two or three streamside species over most or all of the elevational extent of the transect.

Organ extended the analysis to provide detailed data on variation and overlap in microhabitat use of the species. The results verified previous studies documenting the aquatic to terrestrial sequence of large-to-small species in the genus. Although Organ’s study was focused on comparative life histories and population dynamics, rather than interspecific interactions, he interpreted the habitat data within a framework of interspecific competition.

Despite the recognition of many additional species, research in the ensuing 50 yr has strengthened regularities observed by Hairston (1949) and Organ (1961b) in their pioneering studies. Hairston’s student Mark Southerland (1986d) compiled data on assemblage composition in eight stream drainages of the Wilson Creek watershed in the North Carolina Blue Ridge (Table 4). Five drainages supported two streamside and one stream species, and another drainage had three streamside species only. However, two drain-
ages had one streamside and one stream species, and in one of these drainages a single individual of a second stream species (*D. marmoratus*) was observed. Given that some of Southerland’s samples of individual species were small (n = 1–5), it is possible that he missed species in some drainages. At another site in Boone, North Carolina, Southerland (1986b) found that four species occur syntopically, including three streamside forms (*D. monticola, D. fuscus, D. orestes*) and one stream species (*D. quadramaculatus*).

Three stream species occur in the Blue Ridge of northern Georgia and adjacent North Carolina, and they co-occur in some watersheds, usually with two streamside and one forest species (Camp et al., 2002; Camp and Marshall, 2006; Wooten et al., 2010; C. Camp, personal communication; Table 5).

Table 4.—Composition of eight assemblages of *Desmognathus* in the Wilson Creek watershed, North Carolina (Southerland, 1986d). Species are ranked by adult body size (1–5, largest to smallest). Under “Stream” the sequence of numbers (=drainages) follows Southerland (1986d).

<table>
<thead>
<tr>
<th>Species</th>
<th>Life-history category</th>
<th>Body-size rank</th>
<th>Stream 4</th>
<th>Stream 8</th>
<th>Stream 2</th>
<th>Stream 5</th>
<th>Stream 3</th>
<th>Stream 7</th>
<th>Stream 1</th>
<th>Stream 6</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>D. marmoratus</em></td>
<td>Stream</td>
<td>2</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td><em>D. quadramaculatus</em></td>
<td>Stream</td>
<td>1</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td><em>D. monticola</em></td>
<td>Streamside</td>
<td>3</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td><em>D. fuscus</em></td>
<td>Streamside</td>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>x</td>
</tr>
<tr>
<td><em>D. orestes</em></td>
<td>Streamside</td>
<td>5</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
</tbody>
</table>

* Single individual.

In Table 6, I have listed species occurring in 13 watersheds in the Blue Ridge, Cowee, and Nantahala mountains of southwestern North Carolina and nearby areas of the upper Piedmont of South Carolina, based on my surveys over many years (1962–2002). All but one of the watersheds support two streamside species, *D. monticola* and either *D. fuscus/conanti* or *D. ocoee*, and the stream species *D. quadramaculatus*, and these are the only species in seven of the watersheds. Three of the latter watersheds (Bearwallow, Bearcamp, Whitewater) are parallel watersheds of the Blue Ridge escarpment having identical assemblages of *Desmognathus*. However, in the Chattooga watershed to the immediate west of the Whitewater, the stream species *D. marmoratus* and the forest species *D. aeneus* also occur, the latter species sporadically. Piedmont assemblages 1 and 2 formerly occurred in adjacent tributaries of Cane Creek: (1) a lowland, swampy stream with *D. fuscus/conanti* only and (2) an upland stream with three species; both were later destroyed by the construction of Lake Keowee. In watersheds having four, five, or six species, the additions include one stream form (*D. marmoratus*) and two forest species (*D. aeneus, D. wrighti*), added in no particular order.

Interspecific Interactions and the Reality of Intraguild Predation

There is an abundance of experimental evidence that species’ interactions, including interspecific competition and IGP, contribute to the makeup of *Desmognathus* assemblages (reviewed in Bruce, 2007, 2008; Hairston, 1996; Wells, 2007). This evidence can be evaluated within the rich body of recent IGP theory. Several investigators have analyzed the
dynamics of intraguild (IG) interactions by examining external influences on simple three-species IGP modules involving an IG predator, an IG prey, and a resource species (Daugherty et al., 2007; Holt and Huxel, 2007; Holt et al., 2010; Kondoh, 2008; Mylius et al., 2001; Takimoto et al., 2007; Verdy and Amarasekare, 2010). In each, sets of differential equations were used to model population or biomass growth of the modular species and to identify conditions for coexistence and long-term equilibrium. General conclusions derived from three-species IGP modules are that (1) coexistence requires the IG prey to outcompete the IG predator, (2) the IG predator gains significant benefits from consumption of the IG prey, and (3) coexistence of the IG predator and prey is more likely at intermediate levels of resource productivity (Holt and Polis, 1997; Holt et al., 2010: Fig. 18.3). However, the ability of prey to persist under conditions of high productivity has been addressed recently by Abrams and Fung (2010). Moreover, Hall (2011) has shown that the presence of a higher-order predator ("natural enemy") on both the IG predator and prey can promote coexistence if the natural enemy has a greater effect on the IG predator.

A basic IGP module, like those considered in the theoretical studies cited herein, and applicable to any three-member focal group, is shown in Fig. 1A. Most studies of IGP in Desmognathus have been conducted in assemblages of three or more species, usually containing the large D. quadramaculatus as the top predator and at least two IG prey (Table 7). Several modules having an IG predator, two IG prey, and a resource are sketched in Fig. 1. Depending on the strengths of the interactions the outcomes may include coexistence (Fig. 1B), exclusion of one of the IG prey from apparent competition (Fig. 1C), or exclusion of both IG prey if the IG predator is the superior competitor (Fig. 1D). In real assemblages of Desmognathus, a stable coexistence may prevail because the IG prey have refuges and access to exclusive resources or behaviors that reduce the impact of IG predators. For a recent theoretical assessment of the effect of adaptive prey behaviors on stability of IGP systems, see Urbani and Ramos-Jiliberto (2010).

Although theoretical IGP modules often assume that consumer species are specialists on a single resource species, this assumption is unrealistic for many actual systems, such as those involving Desmognathus, given that all species of Desmognathus are opportunistic carnivores that feed mainly on a variety of arthropods and other invertebrates (e.g., Hairston, 1949; Krzysik, 1979; Martof and Scott, 1957). Thus, the food resource must be considered a set of species or a higher taxonomic unit representing a broad, shared food base (e.g., Insecta or Arthropoda).

In the studies of IG interactions listed in Table 7, in evaluating outcomes the larger species was usually considered the predator.
or superior competitor. A landmark study was Hairston’s (1986) experiment on a four-species assemblage, conducted on unenclosed field plots, and designed to examine the effects of removal of one species on density and habitat use of the remaining three. Hairston concluded that predation of both *D. quadramaculatus* and *D. monticola* on *D. ocoee*, and competition between *D. quadramaculatus* and *D. monticola*, were contributing factors in community organization in this assemblage. However, no effect of any of the larger species on *D. aeneus* was detected.
As a second example using a different experimental design, Fauth (1998) used common-garden experiments to investigate the effects of adults of the larger species *D. quadramaculatus* and *D. monticola* (predators) on the smaller species *D. fuscus* (prey). Sources were allopatric and sympatric populations of the three species. Fauth found, in general, that naïve *D. fuscus* from outside the range of either predatory species showed less avoidance behavior, suffered greater mortality and injury, or both, than *D. fuscus* sympatric
with either larger species. This finding suggested that sympatric *D. fuscus* had evolved defenses to counter depredation by *D. quadramaculatus* and *D. monticola*. Thus, the incidence of IGP may be low and the strength of the interaction link may be weak in such assemblages. Numerous other experiments using various designs cited in Table 7 also have identified IG predation (but mainly the threat of predation) of a larger on a smaller species as a factor in community organization in the genus.

In those other studies that provide evidence of competition, the interaction has usually been ascribed to aggressive interference rather than exploitative competition (e.g., Keen, 1982). The response variable in many of these studies was some feature of the physical habitat, especially substrate and cover objects (rocks, wood), rather than food (Carr and Taylor, 1985; Keen, 1982; Kleeberger, 1984; Kissler et al., 2004; Roudebush and Taylor, 1987). Kleeberger (1984), however, linked the two by suggesting that in *D. monticola* there might be a correlation between the density of essential habitat components (rocks on streambanks serving as cover objects) and that of invertebrate prey that represent the salamanders’ food source and also find cover under rocks. Krzysik (1979) and Holomuzki (1980) have compared diet and foraging activity, respectively, in sympatric streamside *Desmognathus*, in each case concluding that differences were sufficient to minimize competition for food and thus contributed to the observed levels of coexistence and habitat overlap. Several experimental studies failed to find evidence of interspecific competition or predation (Grover, 2000; Keen, 1985; Kleeberger, 1984); in some cases, these results may reflect lack of interaction under the constraints of the experimental designs. In cases listed in Table 7 where the interpretation of the author was unclear, I have included a (?). For example, Southerland published four studies in 1986 that reported on interactions among four species using a variety of experimental protocols. His interpretation focused on predation, but several of the outcomes could have been interpreted as effects of competition. Overall, however, given the body of evidence of a sufficiently large number of diverse studies, interspecific competition and IGP seem to be important contributors to the organization of *Desmognathus* assemblages.

There is some evidence of stage- and size-mediated variation in responses between species. Theoretical models of such relationships were provided by Mylius et al. (2001), based on the Holling type II functional response. The authors examined conditions for coexistence (equilibrium) in simple three-species stage- and size-structured IGP modules (Fig. 2).

In one scenario, IG predators may feed on smaller, younger IG prey, but as surviving IG prey grow larger the relationship shifts to competition (Fig. 2A). Southerland (1986a, c) reported that large, adult *D. quadramaculatus* represent a predatory threat to juveniles of the smaller species, especially *D. monticola*, but that the relationship between adults of the two species may shift to interference competition, favoring the larger *D. quadramaculatus*, rather than outright predation. Southerland detected no evidence that large, adult *D. monticola* prey on small, juvenile *D. quadramaculatus* (which are relatively large at metamorphosis). In a second scenario, the relationship between the IG predator and IG prey may involve competition when young, small IG predators are similar in size to the IG prey, but shifts to predation as the IG predators grow to larger sizes (Fig. 2B). Both Southerland’s (1986c) results for the *D. quadramaculatus–D. monticola* pair and Carr and Taylor’s (1985) results in the pairs *D. quadramaculatus–D. monticola* and *D. monticola–D. ocoee* suggested that interference competition occurs between smaller, similar-sized individuals, with a shift to predation as individuals of the larger species in each pair outgrow those of the smaller species. The two scenarios can be combined into a single scenario based on the patterns of growth in the species involved (Fig. 3). And in the modules illustrated in Figs. 2 and 3, and their expression in *Desmognathus*, shift in resource use with growth in either species would be expected to change the dynamics of competition between them for the common resource that in *Desmognathus* may include either the invertebrate food base or habitat elements.
(refuges, cover objects), or, as suggested by Kleeberger (1984), a combination of the two resources.

Southerland’s (1986a,c) results suggested that in the *D. quadramaculatus*–*D. monticola* pair the former species is the superior competitor as well as a predator of the latter; however, in IGP theory coexistence requires the prey to be competitively superior to the predator, and the predator to obtain significant benefits from consumption of the prey (Holt and Polis, 1997). Yet *D. monticola* is an abundant species in many assemblages where its role is that of a middle species, positioned between the larger *D. quadramaculatus* and smaller species such as *D. fuscus* or a member of the *D. ochrophaeus* complex. Thus, it seems likely that internal linkages ($\alpha_3$) of *Desmognathus* IGP modules are weaker than the external links ($\beta_3$) with other components of the ecosystem. Regardless, the evidence in *Desmognathus* for size-mediated shifts in interaction modes is inconclusive (e.g., see Roudebush and Taylor, 1987). There is, in fact, little direct evidence for significant IG predation in nature (Camp, 1997; Krzyzsk, 1979; Martof and Scott, 1957), although the risk of predation (“fear”) may represent an important factor in the regulation of assemblage structure in *Desmognathus*, as in other systems (Berger, 2010).

None of the studies listed in Table 7 included larval phases. Theoretically, abundant species with complex life cycles (most *Desmognathus*) that have strong linkages across ecosystem boundaries (stream and forest) can serve as sources of spatial variation in the impacts of interspecific interactions (McCoy et al., 2009; Schreiber and Rudolf, 2008). McCoy et al. (2009) have referred to the influx of metamorphosing predators from aquatic larval habitats as a “predator shadow” of consumption on the prey in the adjacent terrestrial ecosystem (e.g., McCoy et al., 2009: Fig. 1d). Variation in productivity or mortality in the habitat used by one or another life-history stage of the predator can influence the magnitude of predation in the habitat used by the succeeding stage and thus can result in apparent competition between prey species in different habitats. Understanding the dynamics and resultant equilibrium conditions of interspecific interactions involving competition and intraguild predation requires inclusion of

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**Fig. 2.—** (A) Size- and stage-mediated intraguild predation (IGP) module in which small, young consumers are eaten by the predator but eventually grow to sizes invulnerable to the predator. (B) Size- and stage-mediated IGP module in which consumers and smaller, younger predators compete for the resource, but predators outgrow consumers and become predatory on them.

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$\text{A}$

\[ \begin{array}{c}
C_2 \\
\text{growth} \\
C_1 \\
\end{array} \]

$\text{P}$

$\text{R}$

---

$\text{B}$

\[ \begin{array}{c}
P_2 \\
growth \\
P_1 \\
\end{array} \]

$\text{P}$

$\text{R}$

---

$\text{A}$

$\text{B}$
all life-history stages of the species in question in theoretical models and in experimental protocols that cross the boundaries of the relevant ecosystems.

Ecological factors other than IG interactions that affect the composition of *Desmognathus* assemblages include the role of geographic and climatological history in the speciation process; dispersal; variation in the physical environment (e.g., precipitation, temperature, hydrology); and the wider biotic environment, including prey resources, extralimital predators, and competitors among other plethodontid genera (e.g., *Eurycea*, *Gyrinophilus*, *Pseudotriton*, *Plethodon*).

Current understanding of interactions among coexisting species of *Desmognathus* leaves many unresolved questions. Interactions between some pairs of similar syntopic species (e.g., *D. marmoratus*–*D. quadramaculatus* and *D. aeneus*–*D. wrighti*) have not been studied experimentally. Larval interactions have not been investigated, but they might be especially important in syntopic pairs of species with lengthy larval phases, such as *D. marmoratus*–*D. quadramaculatus* and *D. quadramaculatus*–*D. folkertsi*. There is evidence that one other plethodontid, *Eurycea wilderae*, that coexists with aquatic species and stages of *Desmognathus* is regulated in the larval stage by bottom-up factors originating in the allochthonous detritus of mountain streams (Johnson and Wallace, 2005); these authors suggested that populations of larval *Desmognathus* are similarly regulated.

One enigmatic aspect of variation in assemblage structure in the southern Blue Ridge is the distribution of the two largest and most aquatic species, *D. marmoratus* and *D. quadramaculatus*. The distribution of the former is
a patchwork within part of the range of the latter. Thus, in watersheds of appropriate order (i.e., third order) the Desmognathus assemblage includes either *D. quadramaculatus* or both *D. quadramaculatus* and *D. marmoratus*, as alternative states, as well as various other species of the genus. Desmognathus marmoratus is absent from numerous watersheds where the habitat seems suitable. Although the genetic relationships of the two species are complex (Jones et al., 2006), in streams where both occur they readily sort into two similar but distinctive forms that are apparently reproductively isolated. Jones et al. (2006) suggested that the distribution of *D. marmoratus* is a consequence of geologic changes, including stream captures, in Appalachian river drainages.

The ecological relationships of *D. marmoratus* and *D. quadramaculatus* are poorly understood. Martof and Scott (1957) compared the diets of metamorphosed individuals (juveniles and adults) only and found that *D. quadramaculatus* feeds on more terrestrial prey than *D. marmoratus*, mainly insects but also other salamanders (2.5% of 119 items; species not identified). These authors did not compare diets of larvae in syntopic populations, but it seems that there is broad overlap between the species in larval food habits (cf. Davic, 1991: Table 1 and Martof and Scott, 1957: Table II). Larvae of the two species overlap broadly in size although *D. quadramaculatus* has a lengthier larval period and metamorphoses at larger sizes than *D. marmoratus* (Bruce, 1985).

Can *D. marmoratus* and *D. quadramaculatus* be considered an IGP focal group of stream species? Both species are reported to include small numbers of salamanders in their diets in nature (Camp, 1997; Davic, 1991; Martof and Scott, 1957); however, Camp (1997) concluded that *D. quadramaculatus* is an insignificant predator on other Desmognathus. Nevertheless, in syntopic populations, where *D. quadramaculatus* grows to larger sizes than *D. marmoratus* in both the larval and adult stages, it is likely that it represents a greater predatory threat to *D. marmoratus* than the reverse. Thus, if *D. marmoratus–D. quadramaculatus* form an IGP module, alternative states are *D. quadramaculatus* alone and coexistence. Ecological theory predicts the former state (IG predator only) at high resource productivities and the latter state (coexistence of IG predator and prey) at intermediate productivities (Takimoto et al., 2007; Verdy and Amarasekare, 2010). Whatever the historical explanation of the distribution of *D. marmoratus* in comparison with that of *D. quadramaculatus* (Jones et al., 2006), the current distribution of the species could be examined experimentally to investigate the possible roles of competition and predation in their ecology. Given the variation in Desmognathus assemblage structure over the conjoint range of *D. marmoratus–D. quadramaculatus*, I suggest that the presence–absence of most other species, with the exception of *D. folkertsi* in northern Georgia (Wooten et al., 2010: Fig. 1), which coexists in some streams with *D. quadramaculatus* and *D. marmoratus* (C. Camp, personal communication), has little influence on the interaction between these species.

**Community Assembly**

Evidence, although incomplete, of a significant role of interspecific competition and IGP as organizing factors in Desmognathus assemblages allows the formulation of a stepwise niche assembly model, as promulgated by Adams (2007), Brown et al. (2002), and Fox (1987), to explain variation in assemblage composition. Thus, unitary “assemblages” of Desmognathus invariably consist of one streamside species. Two-species assemblages ordinarily contain streamside species only. Some three-species assemblages include only streamside forms, whereas others contain two streamside and one stream species. Addition of a fourth species to such assemblages would likely involve a stream species in the former assemblages and a stream or streamside form in the latter assemblages. The fifth and sixth species would usually be either stream or forest species. The maximum numbers are two or three streamside, two or three stream, and two forest species. However, assemblages of more than six species are undocumented but may exist in the Great Smoky Mountains of North Carolina and Tennessee and in the southern Nantahala Mountains along the North Carolina–Georgia border.
Exceptions to the patterns generated by the above-mentioned model involve the forest species *D. aeneus*, *D. organi*, and *D. wrighti*. For example, *Desmognathus* assemblages are attenuated at the highest elevations of the southern Blue Ridge, consisting of a forest species, such as *D. organi* or *D. wrighti*, and one or two streamside species, such as *D. imitator*, and a member of the *D. ochrophaeus* complex. At low elevations, the range of the forest species *D. aeneus* extends southwestward from the Blue Ridge into central Alabama where it co-occurs with the streamside species *D. conanti* and *D. monticola*. In both of these cases, a stream species would have been expected before the addition of a forest species, but the former species may be excluded because of climatological or hydrologic limits relative to the adaptive zones of extant stream species.

There are several problems with the application of this assembly rule model in *Desmognathus*. First, such rules are sometimes formulated in terms of evenness, whereby species are added to communities from different functional groups or guilds before additional members of the same group are added, as proposed by Adams (2007) for eastern *Plethodon*. Communities that are perfectly even or differ by no more than one species from evenness are said to be in a favored state. Under the criterion adopted herein for recognizing functional groups based on life-history categories (i.e., larval period), this rule does not apply to *Desmognathus* because of the prevalence of streamside species in all assemblages and the occurrence of as many as three streamside species only in some.

More importantly, the formation of extant *Desmognathus* assemblages is unlikely to have occurred in a straightforward stepwise manner as proposed by the niche assembly model outlined herein. For example, a three-species assemblage of two streamside and one stream species may have been “disassembled” by local extinction of a third streamside species, either by deterministic factors (e.g., predation or competitive exclusion) or stochastic events (e.g., random extinction of small populations), rather than assembled by addition of a stream species. Thus, these assemblages are ostensively the result of complex episodes of dispersal, vicariance, and speciation–extinction, modulated by IG competition and predation, and by extralimital interactions, especially with sympatric clades of *Plethodon* and spelerpine plethodontids. These processes have operated within the framework of environmental and climatological changes in eastern North America during the past 20–30 million yr. The possible influence of such factors on *Desmognathus* evolution and community assembly has been addressed by K. Kozak and colleagues in several studies (Kozak and Wiens, 2006; Kozak et al., 2005, 2009).

The restriction of the relatively few forest and stream species to the southern Appalachian Mountains and immediate environs, with the occurrence of the more numerous streamside species throughout the range of the genus, requires further consideration. Seemingly, the streamside mode of life has engendered greater dispersal abilities and greater plasticity in adaptation to the environmental extremes of temperature and moisture than in the forest and stream species. That two streamside species (*D. fuscus*, *D. ochrophaeus*) alone extend their ranges well north of the boundary of the Wisconsin glacial maximum may attest to the greater dispersal abilities of streamside forms. Dispersal in the forest and stream species may be constrained by the requirements for mesic forests by the former and relatively permanent stream flow by the latter, conditions which are afforded by temperate southern Appalachian environments that promote the coexistence of multiple species of all three life-history categories.

**DISCUSSION**

Until recently, a widely accepted hypothesis of *Desmognathus* phylogeny posited the derivation of increasingly terrestrial lineages from more aquatic ancestors (Dunn, 1926; Hairston, 1949; Wake, 1966). Later, I suggested that streamside species represented the ancestral mode of life and that both the aquatic and terrestrial species were derived (Bruce, 1991). Recent molecular phylogenetic analyses have suggested that ancestral *Desmognathus* were in fact terrestrial, having direct development, and that evolution in the genus has involved the derivation of a complex life
cycle with an aquatic larval stage (Beamer and Lamb, 2008; Chippindale et al., 2004; Kozak et al., 2005, 2009; Macey, 2005; Mueller et al., 2004; Titus and Larson, 1996). This process is considered a reversal, inasmuch as ancestral salamanders and probably ancestral plethodontid had complex life cycles, with direct development a derivative state in several plethodontid lineages. Wake et al. (2011) cited this process as an example of homoplasy by reversal. The hypothesis of life-history reversal in Desmognathus is based on (1) the nesting of the genus in a clade of direct-developing taxa; (2) the terrestrial life cycle of Phaeognathus hubrichti, the sister taxon of Desmognathus; and (3) the basal position of one or more of the terrestrial species of Desmognathus, but especially of D. organi–D. wrighti, in the multiple phylogenetic studies cited herein.

Streamside species form the base of Desmognathus assemblages throughout the range of the genus in eastern North America. Streamside species alone occur on the periphery of the range. Assemblages of two or more species of Desmognathus invariably contain streamside species, usually two or three, with or without the presence of stream species, forest species, or both. Although many unresolved questions remain, there is strong experimental evidence that interspecific interactions, including competition and IGP, contribute significantly to the organization and species richness of Desmognathus assemblages. Therefore, niche assembly, as a constituent process within the framework of the unified neutral theory, seems to be a valid model for evaluating assemblage organization in the genus. Theoretically, in niche-assembled communities species coexist in an interactive equilibrium with one another and form a tightly organized unit that resists perturbation and invasion (Hubbell, 2001).

The evenness criterion used by Adams (2007) to evaluate Plethodon assemblages in eastern North America does not apply to niche assembly in Desmognathus, given that the first two or three species to be included in an assemblage are streamside species. Moreover, biogeographic and ecological evidence suggests that community assembly in the genus cannot be accounted for through the simple, stepwise addition of species of alternative life-history categories. Rather, as discussed above in Community Assembly, adaptive radiation and community assembly have probably been driven by a complex interplay of multiple processes, promoting episodes of assembly, disassembly, and reassembly, under the influence of climatological and environmental fluctuations in eastern North America since the Miocene. However, in any historical scenario, streamside forms have undoubtedly played a formative role in community assembly of Desmognathus. Their dominance in species number, their numerical abundance in many assemblages, their occurrence throughout the entire range of the genus, and their sole occupancy of the periphery of the distribution of the genus all suggest that early adoption of a streamside mode of life, whether ancestral or not, was a key factor in diversification of Desmognathus.

Molecular studies of Desmognathus phylogeny suggest that the genus underwent a rapid phase of diversification and speciation (“ecomorphological diversification”) beginning in mid-Miocene (Kozak et al., 2005). Recent phylogenetic analyses indicate that many additional lineages may deserve species recognition (Beamer and Lamb, 2008). This diversification has been generated within constraints prescribed by the unique synapomorphies and morphological conservatism of the genus (Schwenk and Wake, 1993; Sweet 1973, 1980). As noted, such constraints, acting within a suite of species varying markedly in body size, ecology, and life history, suggest that life histories of Desmognathus incorporate a high level of symmetry, as defined by Charnov (1993), that is expressed in the observed trade-offs among species and among populations within species. A key parameter contributing to variation in adult body size is age at first reproduction, because in Desmognathus growth declines at sexual maturation (Bruce, 2009, 2010), especially in females (Hom, 1988; Tilley, 1980). Under the assumption that selection acts to maximize net reproductive rate ($R_0$), optimal age at first reproduction is a function of mortality rate, the size–fecundity relationship, propagule size, and growth rate (Roff, 1984, 2002: pp. 217–221). Selective pressures on age at
first reproduction arising from shifts in predation, parasitism, competition, resources, and the physical environment that affect mortality rate may elicit responses that reset the values of such other parameters as propagule size and fecundity, as trade-offs within a common set of constraints prescribed by the morphological specializations and conservatism of the genus. Thus, a high degree of symmetry in life-history traits may have played a key role in the rapid initial radiation of *Desmognathus*, enabling the life-history diversification that paralleled diversification in body size, as lineages exploited the ecological opportunities of the aquatic-to-terrestrial habitat gradient. Testing of the symmetry hypothesis will require a wealth of additional comparative data on life history and demography in *Desmognathus*, especially (1) among species within assemblages, wherein the component species experience common climatological and hydrologic regimes, as well as (2) within species among assemblages that are subject to different environmental regimes.

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