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Spatial Distributions of Three Species of *Desmognathus* in a North Carolina Stream

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Abstract

Salamanders of the family Plethodontidae comprise the most common salamanders in eastern North America. It is not uncommon for more than 10 plethodontid species to occur syntopically in one creek. The purpose of this research was to determine whether the spatial distribution of one species affected the spatial distribution of other species. Geographic Information System technology and nearest-neighbor analyses were used to determine the spatial distributions of three species of the salamander genus *Desmognathus*. The analysis demonstrates that *D. ochrophaeus* and *D. monticola* change their spatial use from a random distribution during the day to a clumped distribution during evening hours. The data also suggest the *D. monticola* moves into the creek during evening hours.

Introduction

Over the past 40 years, salamander communities have provided excellent experimental systems for ecological experimentation on community organization (Hairston, 1949, 1986; Kleeberger, 1984; Roudebush and Taylor, 1987; Formanowicz and Brodie, 1993) because they provide the researcher long-lived animals with stable populations. Furthermore, salamander communities conform to many of the assumptions necessary for the theories of community organization and of evolution under the influence in interspecific interactions.

The plethodontid salamander genus *Desmognathus* consists of a series of species whose ecological preferences range from aquatic to semi-terrestrial. Concomitant with the particular species' ecological preference are morphologies, size ranges, and behaviors (Dunn, 1926; Hairston, 1949; Formanowicz and Brodie, 1993). In the southern Appalachian Mountains of eastern North America, communities of salamanders usually contain four to seven species of *Desmognathus* in addition to salamanders of three to five other plethodontid genera. Generally, the most terrestrial species is smallest, most brightly colored, and possesses the least keeled tail, whereas the most aquatic species is the largest, most heavily pigmented, and possesses the most fish-like tail. Species inhabiting intermediate ecological positions generally possess intermediate characteristics (Dunn, 1926).

In this study the relative positions of individuals of three species of *Desmognathus* in a North Carolina creek were analyzed. We investigated the following three species: (1) *D. quadramaculatus*, the largest and most aquatic salamander in the community; (2) *D. monticola*, an intermediate-sized species preferring aquatic environments

(Roudebush and Taylor, 1987); and (3) *D. ochrophaeus*, a small, semi-terrestrial species. Specifically, our goal was to determine the feasibility of using Geographic Information System (GIS) technology to determine the following: (1) the spatial distribution of individuals of these three species; (2) whether diurnal spatial distribution could be differentiated from nocturnal spatial distribution; and (3) whether differential species' movements could be determined.

Methods and Materials

Field methods.--During the spring of 1993 (20 - 28 May), the Advanced Field Biology class from the University of Arkansas - Little Rock conducted the field experiment in Kinsey Creek, Deep Gap Vista, Macon Co., North Carolina. The headwaters of the creek form from a series of seepage areas that coalesce into a permanently flowing creek. A position approximately 50 m downstream from the seepage areas was selected. At this location the creek was clearly identifiable. A 90-m transect through the center of the creek served as a baseline to establish study plots. Each study plot was 10 m in length (along the creek) and 3 m wide (perpendicular to the axis of the creek.) Nine continuous 3 m by 10 m "creek-plots" were determined in this manner. Numbered surveyor's flags were used to demarcate the corners of each study plot.

Teams of students systematically searched plots by carefully observing the surface and by gently turning over and replacing rocks and debris. When a salamander was found, it was identified by species, and its position was marked by a color-coded surveyor's flag. Different colored flags were used for daytime and nighttime positions so

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that a field map could be constructed for the study area. Ninety square meters of the total transect were searched each day (once diurnally and once nocturnally) for three consecutive days, for a total of 270 m² of study area.

Analytical Methods.--Geographic Information System ARC/INFO (ESRI, 1989) was used to digitize field maps into the computer. Once digitized, the data were translated into a planar coordinate system and scaled. Relative coordinates for salamander locations were used to construct analytical maps. Those coordinates were extracted and used for statistical analysis. Study maps were plotted using the animals' coordinates in the creek as points. A grid of 1 m² was superimposed on the study map. Each 1 m² was considered a sample unit for statistical analysis.

Statistical analysis involved two general analytical protocols. First, to determine the spatial distribution of the animals in the study area, their observed distribution was compared to a Poisson and a Negative Binomial distribution; Chi-square was used as the test statistic (Ludwig and Reynolds, 1988). Second, to determine the relationships between the positions of individuals with respect to other individuals or to the boulder centroids, nearest-neighbor analysis (Cressie, 1991) was used. To compare daytime nearest-neighbor distributions with nighttime nearest-neighbor distributions, the degrees of freedom were adjusted for non-independence, and analysis of variance (Legendre, 1993) served as the test statistic.

Results

During the three-day study period, a total of 346 salamander observations were recorded from the 270 m² of creek sampled. Because the study did not involve the removal of individuals, the number of unique salamander sightings was not determined. Nighttime observations accounted for 63% of all observations, whereas daytime observations accounted for 37% of the total. Although the number of *D. quadramaculatus* observations did not differ significantly between day and night (35 daytime: 43 nighttime; Chi-square = 0.82, ns), the number of *D. monticola* (31:103; Chi-square = 77.9, $P < 0.05$) and the number of *D. ochrophaeus* (54:79; Chi-square = 4.68, $P < 0.05$) sightings indicated significantly more nighttime observations were made.

The distribution of boulder centroids and salamanders was compared to a Poisson distribution. As the variance/mean ratio (= index of dispersion) was very close to 1, $|d|$ (= the index of dispersion) was less than 1.96, and Chi-square value was not significant (Table 1), therefore the hypothesis that the boulders follow a Poisson distribution (=random) in the study area can not be rejected. Similarly, on an individual basis, each species is randomly distributed (i.e., variance/mean ratios are near unity, $|d|$

less than 1.96, and not significant Chi-square values) during the daytime (Table 1). However, the observed distributions for *D. monticola* and *D. ochrophaeus* indicate a significant (variance/mean ratio greater than 1, $|d| > 1.97$, Chi-square, $P < 0.05$) departure from expected values during the nighttime (Table 1). The direction of the departure suggests a clumped pattern, as indicated by the variance/mean ratios being greater than 1.0. Therefore, a comparison of these two distributions to a negative binomial was made. Chi-square values for *D. monticola* (Chi-square = 3.30, df = 2) and *D. ochrophaeus* (Chi-square = 4.59; df = 2) evening observations do not permit us to reject a departure from the negative binomial distribution.

Table 1. Spatial distribution of three species of *Desmognathus* in a North Carolina creek, May, 1993 compared to a Poisson distribution.

	Chi-Square ¹	d ²	Variance: Mean ratio
Boulders	1.59 ns	0.609	1.05
<i>Desmognathus monticola</i>			
day (31)	0.07 ns	1.07	1.09
night (104)	10.56*	4.84	1.45
<i>Desmognathus ochrophaeus</i>			
day (54)	0.09 ns	1.15	1.10
night (79)	8.77*	7.36	1.72
<i>Desmognathus quadramaculatus</i>			
day (43)	0.09 ns	0.90	1.07
night (35)	0.01 ns	0.11	0.98

1- minimum of 5 observations per cell, df varied with case.

2- index of dispersion

* $P < 0.05$, ns = not significant

The results of the nearest-neighbor analysis indicate that the distances recorded at night and those recorded during the day between *D. quadramaculatus* and boulder centroids do not differ significantly (Table 2). Similarly, the nearest-neighbor distances between *D. quadramaculatus* and *D. ochrophaeus* do not change night vs. day. However, the nearest-neighbor distances between *D. quadramaculatus* and *D. monticola* are significantly smaller ($F_{1:38} = 23.29$, $P < 0.05$) at night (Table 2), as are the nearest-neighbor distances between *D. monticola* and *D. ochrophaeus* ($F_{1:66} = 16.22$, $P < 0.05$). To account for the difference in number of sightings (day vs. night), 20 inter-individual distances were randomly selected and the data reanalyzed. For each case there were no qualitative difference between the random sample and the entire data set.

Table 2. Nearest neighbor distances for three species of *Desmognathus* in Kinsey Creek, North Carolina.

Species	<i>Desmognathus monticola</i>	<i>Desmognathus ochrophaeus</i>	<i>Desmognathus quadramaculatus</i>
Boulders			
day	1.26	1.33	1.12
night	1.15 ns	1.08 ns	1.17 ns
<i>Desmognathus monticola</i>			
day (31)	1.96	2.30	2.51
night (104)	0.48 *	0.72 *	0.77 *
<i>Desmognathus ochrophaeus</i>			
day (54)		0.71	1.38
night (79)		0.72 ns	1.54 ns
<i>Desmognathus quadramaculatus</i>			
day (43)			1.02
night (35)			1.65 ns

* $P < 0.05$, ns = not significant

Discussion

Theories of community organization based on competition and niche partitioning (Hutchenson, 1959) have been challenged on several grounds (Simberloff, 1980; Hairston, 1986). The discussion of eco-evolutionary factors influencing desmognathine community structure and evolution began with Dunn's (1926) hypothesis linking *D. quadramaculatus*, by virtue of its creek-bed habitat, to the prototypical *Desmognathus*. In Dunn's phylogeny, terrestriality evolved as a response to competition pressure for optimum mid-creek habitat. Thus Dunn (1926) interpreted competition to be the single force that molded both evolution and community structure. Later, Hairston (1949) and Organ (1961) investigated desmognathine salamander communities and followed Dunn's interpretations.

However, Hairston (1980) re-evaluated his earlier conclusions concerning community structure resulting from competition in light of the assumptions for the competition models and the absence of experimental data. Hairston constructed a series of nine predictions based on the competition model. Of these, only three were confirmed. Competition appeared to be inadequate to explain or to describe the *Desmognathus* community. In this analysis, Hairston (1980) could produce no evidence for competition and invoked predation as the only eco-evolution-

ary force in desmognathine communities.

In a later paper, Hairston (1986) presented the results of four years of his experimental field removal studies. He constructed several specific hypotheses that could differentiate between competition and predation. Hairston (1986) demonstrated that both *D. monticola* and *D. quadramaculatus* were predators of *D. ochrophaeus*. This led him to suggest and demonstrate that if *D. ochrophaeus* were removed, *D. monticola* and *D. quadramaculatus* would compete. He concluded that both competition and predation occur within this apparently well-defined guild and warned of the danger of a casual interpretation of ecological observations.

Although the data from this study do not directly address either predation or competition, they do provide further evidence that the community spatial structure changes on a daily basis. Unlike the data presented from field enclosures (Southerland, 1986a; b), these observations were made in an unrestricted environment. Furthermore, although the data in this study do not differentiate between adult and juvenile individuals, all larvae (individuals under 3 cm snout-vent length) were excluded from our analyses.

It appears that the distribution of *D. quadramaculatus* in the creek is not influenced by other species' distributions. Its distribution with relation to the optimal boulder habitat (Roudebush and Taylor, 1987) did not change. However, the distributions of both *D. monticola* and *D. ochrophaeus* were observed to be clumped and individuals of both species appeared significantly closer to each other (Table 2) at night. Although the change in the distribution does not indicate a cause, several hypotheses can be constructed and tested. The purpose of this study was to determine the feasibility of using GIS to investigate the distributional aspects of community ecology and this has been accomplished.

The changes in distribution observed are consistent with the direction of change observed by Southerland (1986b) for enclosed *D. monticola* trials. It is suggested that *D. monticola* move from the forest floor into the creek at night. However, there was no observation of a concomitant decrease in the number of *D. quadramaculatus* or a shift in the position of *D. quadramaculatus*, as was suggested by Southerland (1986b). In fact, the number, position, and random distribution of *D. quadramaculatus* did not change, so no inference about either competition or predation can be made to account for the movements of *D. monticola*. Again, to eliminate competition or predation, specific removal experiments will need to be performed. If, for example, the removal of *D. monticola* results in *D. quadramaculatus* venturing further from the center of the creek (as determined by differences between day and night distances from boulder centroids), then competition is involved in generating the observed spatial distribution.

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Similarly, if the removal of *D. ochrophaeus* intensifies the competition between *D. monticola* and *D. quadramaculatus* (as determined by increased clumpedness), then well defined patches of these species should be apparent in the creek. These and other experiments are currently in the planning stage.

Finally, the observations of this study were directed at only the 90 by 3 m area contained within the creek bed. Hairston (1949, 1980, 1986) and others included the forest floor up to 15 m from the creek and measured average distances from the creek. Incorporation of these additional habitats may provide additional insights into the diurnal and nocturnal dynamics and specific interactions in this community.

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