SUBSTRATE SELECTION BY THREE SPECIES OF DESMOGNATHINE SALAMANDERS FROM SOUTHWESTERN PENNSYLVANIA: AN EXPERIMENTAL APPROACH

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ABSTRACT

An experimental technique is developed to quantify substrate selection by stream-bank salamanders. Substrate particle size has been shown in field studies by the senior author to be an important niche parameter. Interspecific differences in substrate size selection is hypothesized to play a central role in determining coexistence patterns and habitat selection in Desmognathus. Substrate selection experiments in the laboratory are desirable for controlling field variables and critical to understanding community organization in these salamanders.

INTRODUCTION

Researchers have studied interactions between species of salamanders in the laboratory (Jaeger, 1974; Thurow, 1975, and others) but the study of substrate selection has been ignored. There is theoretical (MacArthur and Pianka, 1966) as well as empirical (Schoener, 1974) justification for hypothesizing that differential microhabitat utilization by coexisting community members is usually the most important factor permitting stable coexistence and minimizing actual or potential competition. Krzysik (1977) found a strong intra- as well as interspecific

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Table 1. — Substrates and their particle sizes utilized in substrate selection experiments.

<table>
<thead>
<tr>
<th>Substrate</th>
<th>Particle size</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sand</td>
<td>0.05–0.5 mm</td>
<td>Fine construction sand¹</td>
</tr>
<tr>
<td>Small gravel</td>
<td>0.5–1 cm</td>
<td>1B construction gravel</td>
</tr>
<tr>
<td>Medium gravel</td>
<td>1.5–3 cm</td>
<td>2B construction gravel</td>
</tr>
<tr>
<td>Large gravel</td>
<td>4–8 cm</td>
<td>Hand selected round and smooth glacial</td>
</tr>
<tr>
<td></td>
<td></td>
<td>deposit rocks</td>
</tr>
<tr>
<td>Rocks</td>
<td>8–15 cm by 1–3 cm</td>
<td>Hand selected flat sedimentary rocks,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>comprising the rubble of stream-banks</td>
</tr>
</tbody>
</table>

¹ A few small rocks (1–2 cm) were sprinkled on the surface, otherwise this substrate was totally avoided by salamanders.

(particularly the latter) relationship between body size and substrate selection by salamanders in the field, and showed that substrate particle size is an important microhabitat parameter determining coexistence patterns within a desmognathine salamander community.

Substrate selection experiments under laboratory conditions are desirable because of the large number of uncontrollable variables in the field. Substrate size is easily controlled, and such important field variables as microhabitat moisture, distance from the stream, size and type of cover, and others may be eliminated. A firm experimental basis for intra- and interspecific substrate relationships among desmognathine salamanders is important in understanding coexistence patterns and microhabitat resource allocation in this community. This report represents a preliminary investigation of an experimental procedure for quantifying substrate size selection by streambank salamanders, utilizing three sympatric desmognathines from southwestern Pennsylvania.

**Materials and Methods**

Nine all-glass aquaria (76 cm by 30 cm by 30 cm) were separated into three 25 cm by 30 cm compartments by plexiglass dividers. The dividers were 10 cm high and several 3 mm holes were drilled into each so that an equal water level could be maintained. Each of the three compartments was filled to the top of the divider with the substrates that were being compared. Water was added to each aquarium until it reached a depth of 2 to 3 cm below the surface of the substrate. A square board 10 cm on a side and 1.3 cm thick was placed in the center of each compartment. The board was raised about 1 cm over the substrate when sand or fine gravel was utilized as the substrate. The tanks were carefully sealed with aluminum foil containing small vents to provide limited air flow. Thus a high humidity was constantly maintained in all tanks (>90%) and all substrates utilized were constantly wet. Five different substrates, which formed a particle size gradient, were utilized (Table 1). A sixth "substrate", the glass sides of the aquaria, was additionally considered.

Three species of sympatric salamanders (*Desmognathus monticola*, *D. fuscus*, and *D. ochrophaeus*) were collected at Rachelwood Wildlife Research Preserve (Westmoreland Co., southwestern Pennsylvania). Animals used in the study were anesthetized in a
The species of Desmognathus and their respective body sizes used in the study.

<table>
<thead>
<tr>
<th>Species</th>
<th>Snout-vent length (mm)</th>
<th>Total length (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>D. monticola</em> (♂ ♀)</td>
<td>68-74</td>
<td>124-136</td>
</tr>
<tr>
<td><em>D. fuscus</em> (♂ ♀)</td>
<td>60-68</td>
<td>99-125</td>
</tr>
<tr>
<td><em>D. monticola</em> (immature)</td>
<td>45-51</td>
<td>80-105</td>
</tr>
<tr>
<td><em>C. ochrophaeus</em> (♂ ♀)</td>
<td>41-45</td>
<td>77-93</td>
</tr>
</tbody>
</table>

1 Tip of snout to the posterior angle of the vent.

weak solution of tricaine methanesulfonate; snout-vent and total length were recorded, and animals were toe-clipped for identification (Table 2). Animals were stored in moist plastic bags in a refrigerator at 5 to 8°C. Three separate experimental runs were made because only three of the possible substrates could be tested at a time. The three experiments are: 1) sand, medium gravel, rocks; 2) small gravel, medium gravel, large gravel; 3) medium gravel, large gravel, rocks. Tanks were arranged such that each substrate occupied the center compartment of three of the nine tanks. Three mature males (one of each species) were utilized during an experiment. One individual was placed on the board in the center compartment of each tank. Thus the three individuals of any given species were initially placed in compartments that contained each of the three possible substrates. The nine animals were tested for three days under constant darkness with the following routine. Individuals were introduced into the aquaria at around 1000 hrs and were looked for around 2000 hrs (pm observation) with a red light and with minimal disturbance to the substrate. The substrate on which each individual was found was recorded. The following morning (around 0900 hrs—am observation) the individuals were again located, their positions recorded as before and they were removed. This procedure was repeated on two more consecutive days using the same individuals. In this way each individual of each species could initially be placed on each of the three possible substrates. The nine animals were tested for three days under constant darkness with the following routine. Individuals were introduced into the aquaria at around 1000 hrs and were looked for around 2000 hrs (pm observation) with a red light and with minimal disturbance to the substrate. The substrate on which each individual was found was recorded. The following morning (around 0900 hrs—am observation) the individuals were again located, their positions recorded as before and they were removed. This procedure was repeated on two more consecutive days using the same individuals. In this way each individual of each species could initially be placed on each of the three possible substrates. A minimum of six individuals of each species was examined. After the experiments with the mature males were completed, nine immature *Desmognathus monticola* were individually placed in the nine aquaria. They were similarly rotated daily so that each individual was initially placed on each of the three possible substrates.

Model I three-way analysis of variance utilizing arcsine transformations on the frequency data (Sokal and Rohlf, 1969) was used to determine if there were interactions among the three factors—species, substrate, and time of observation (am or pm). Chi-squared goodness of fit (Siegel, 1956) was employed to determine whether or not substrates were differentially utilized. The data from these three experiments were combined (appropriate corrections were made because all substrates were not equally represented after pooling the data) to evaluate the allocation of the substrate microhabitat resource gradient among the members of this hypothetical community of *Desmognathus*. The Kolmogorov-Smirnov two-tailed and one-tailed tests for large samples (Siegel, 1956) were used to determine if any differences or a priori determined directional differences, respectively, were present in substrate selection.

Values of niche overlap (Schoener, 1968) were calculated as

\[ O_{ij} = 1 - \frac{1}{2} \sum |P_{ik} - P_{jk}| \]

where \( P_{ik} \) and \( P_{jk} \) are the proportions of the number of times species i and j were found on substrate k. \( O_{ij} \) can possess values between 0 and 1, indicating no overlap or complete overlap in resource utilization. Niche overlap quantifies the
Fig. 1.—Frequency histograms of four *Desmognathus* body sizes distributed among six substrate categories. See Table 1 for description of substrate categories.

sharing of the substrate resource gradient between two species. Niche breadth (Levins, 1968) was calculated as

$$ B_i = 1 / \sum p_{ik} $$

where $p_{ik}$ is as above. Niche breadth quantifies the diversity or breadth of utilization of the substrate resource gradient by a given species.

**RESULTS**

Analysis of variance of transformed frequency data confirmed that there was no relationship between the time of day the animals were
Table 3.—Values of niche overlap and niche breadth for the utilization of the substrate microhabitat resource gradient.

<table>
<thead>
<tr>
<th></th>
<th>Desmognathus fuscus</th>
<th>Desmognathus monticola (immature)</th>
<th>Desmognathus ochrophaeus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Niche overlap</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D. monticola (mature)</td>
<td>0.911</td>
<td>0.814</td>
<td>0.392</td>
</tr>
<tr>
<td>D. fuscus</td>
<td>—</td>
<td>0.735</td>
<td>0.327</td>
</tr>
<tr>
<td>D. monticola (immature)</td>
<td>—</td>
<td>—</td>
<td>0.572</td>
</tr>
<tr>
<td>Niche breadth</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D. monticola (mature)</td>
<td>2.75</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D. fuscus</td>
<td>2.43</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D. monticola (immature)</td>
<td>3.30</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D. ochrophaeus</td>
<td>4.86</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

observed and either the substrate or the species (P > 0.75); however, there was a significant difference (P < 0.005) in the relationship between a species and the substrate on which it was found. Analyzing all three experiments by $\chi^2$ goodness of fit showed that there was no significant difference in the way that mature D. monticola and D. fuscus males utilized the substrate (P > 0.10) but there was a significant difference among all other combinations (P < 0.001). The data for all substrates were combined and the frequency distribution of the four desmognathines in the six substrate categories is shown in Fig. 1. Again there is no significant difference in the utilization of substrate categories by mature D. monticola and D. fuscus, but there are highly significant differences in all other species combinations (P < 0.02 in the case of mature and immature D. monticola; and P < 0.001 in all other comparisons). Values of niche overlap and niche breadth are given in Table 3.

**Discussion**

Mature males of Desmognathus monticola and D. fuscus, the largest members of the southwestern Pennsylvania desmognathine community, possess a similar preference for the coarsest substrate available (Fig. 1, Table 3). Immature D. monticola can be found associated with substrates possessing a smaller particle size than mature males. Desmognathus ochrophaeus, the shortest and thinnest salamander, was found not only utilizing a wide range of substrate sizes but preferred smaller substrate particle sizes (Fig. 1). This was the only species to show consistent arboreal tendencies. The adaptive significance of substrate selection can be inferred to be the following: large salamanders require larger openings into the substrate to escape predators, locate overwintering cavities, and follow ground water in
periods of drought. Smaller species not only can utilize a wider range of openings for these purposes, but natural selection should favor those individuals that select substrates with smaller openings, hence minimizing predation from larger vertebrates, including other salamanders.

These patterns, along with the fact that body size appears to be an important determinant of interspecific interference competition (Morse, 1974; Thurow, 1975; personal observations), can be used to predict community structure in this genus. *Desmognathus monticola* and *D. fuscus* require habitats possessing a coarse substrate, but because they possess a high overlap in substrate utilization (0.911) *D. fuscus*, the smaller species, should generally be rare in habitats containing the coarsest substrates (for example, those selected by *D. monticola*). When in sympatry with *D. monticola* at habitats which are suboptimal for *D. monticola*, *D. fuscus* should exhibit a shift in microhabitat preference. *Desmognathus ochrophaeus* because of its wide breadth of substrate utilization (4.86) and low overlap with the other species (Table 3) should be an abundant widespread species commonly associated with its congeners, and also found in habitats that are unavailable for the other two species (those with fine substrates). The presence of immature *monticola* in smaller substrates reduces intraspecific competition in this species for shelter and food.

The arboreal tendencies of *D. ochrophaeus* have been observed in the field (Hairston, 1949; personal observations) and may be a mechanism of exploiting food and space resources not utilized by other members of this community. These predicted patterns of desmognathine community organization have been substantiated by field studies (Krzysik, 1977).

**Acknowledgments**

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**Literature Cited**


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