SUBSTRATE CUES INFLUENCE HABITAT SELECTION BY SPOTTED SALAMANDERS

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Abstract: Identifying the cues used by spotted salamanders (*Ambystoma maculatum*) to select forested habitat may provide insight into their habitat requirements and preferences. Environmental factors, such as temperature and moisture, are consistently important factors in explaining the magnitude and timing of annual breeding migrations and are important characteristics of quality terrestrial habitat. These factors, however, may not be used to select terrestrial habitat because microclimate gradients are minimal when salamanders are migrating. To test whether substrates provide cues for habitat selection, we presented juvenile and adult spotted salamanders with a choice between substrates collected from forest or grassland. Further, we presented adults with a choice between litter and a combination of soil and litter collected from forest or grassland. We recorded substrate selection initially and at 3-min intervals for 60 min. Salamanders tended to select the forest substrate more than the grassland substrate in all 4 experiments. Overall, juveniles (88%) selected forest soil more than adults (70%). Adults initially selected forest soil (80%), but the response declined with time. However, when we presented soil and litter in combination, salamanders hid under the litter, and the selection of forest substrate (70%) did not decline with time. The establishment of cues influencing habitat selection provides mechanistic information that may be used to predict habitat selection under scenarios of anthropogenic habitat alteration. Our results suggest that substrate characteristics may influence the presence of salamanders within various habitat types.

JOURNAL OF WILDLIFE MANAGEMENT 68(4):1151–1158

Key words: behavior, choice test, habitat selection, salamanders, substrate cues.

Habitat requirements and preferences of a species may be identified by examining how individuals select habitat. Individuals likely use components of habitat as cues that reliably indicate the quality of the habitat. Habitat selection under natural conditions results from the synthesis of multiple cues (Downes and Shine 1998) and occurs at multiple scales (Johnson 1980). Cues may be biotic (e.g., predator avoidance, conspecific attraction, vegetation preferences, food resources) or abiotic (e.g., temperature, moisture, chemical), and they may originate from a wide variety of sources (e.g., substrate, canopy, other organisms). Identifying the cues used by spotted salamanders to select forested habitats may provide a method for identifying the components of forests that yield suitable salamander habitat.

Adult salamanders emigrate from breeding sites into terrestrial habitats soon after mating, and metamorphosing juvenile salamanders emigrate from early summer through fall. Many studies of amphibian migration have focused on environmental factors correlated with the magnitude and timing of movement (e.g., Joly and Miaud 1993). For ambystomatid salamanders, the time of day, precipitation, and temperature are consistently important factors in explaining migratory activity (e.g., Semlitsch 1985, Semlitsch and Pechmann 1985, Sexton et al. 1990). Although these factors may influence the timing and duration of migration and the number of individuals migrating, they may not provide the cues used for the selection of a migration path or for the selection of terrestrial refuges.

The terrestrial habitat requirements of ambystomatid salamanders are largely unknown and have not been experimentally tested. However, we can assume, based on known physiological and ecological requirements (Feder and Burggren 1992), that salamanders need terrestrial refuges that remain cool in the summer, do not freeze in the winter, and remain moist throughout the year (e.g., Kleeberger and Werner 1983). Spotted salamanders often are described as a highly forest-dependent species (Semlitsch 1985, Semlitsch et al. 1996, Gibbs 1998, Petranka 1998, Semlitsch and Ryan 1999) and are absent from landscapes where the forest canopy cover has been reduced to below 30% (Gibbs 1998). In addition, spotted salamanders avoid grassland (Rittenhouse 2002) and orient toward forests

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(Windmiller 1996, Rittenhouse 2002). Several other amphibian species also orient toward forests, including wood frogs (*Rana sylvatica*; deMaynadier and Hunter 1999), metamorphosing American toads (*Bufo americanus*; Rothermel and Semlitsch 2002), and great crested (*Triturus cristatus*) and smooth newts (*T. vulgaris*; Malmgren 2002).

Although spotted salamanders migrate toward forests, and temperature and moisture are likely important terrestrial habitat requirements, we suggest that temperature and moisture are not the primary cues used in the selection of forested habitat. Spotted salamanders make their annual migrations to and from breeding ponds early in the spring (Sexton 1986), when the ground has recently thawed and may refreeze after salamander migration begins (Madison 1997). The canopy cover does not shade the ground because the leaves have not opened. Thus, air or soil temperature gradients between forested and grassland habitats are minimal in the early spring (Chen et al. 1997). Further, salamanders migrate to and from breeding ponds only during overcast and rainy nights (Semlitsch 1985, Madison 1997, Rittenhouse 2002) when air, soil, and litter are saturated and moisture gradients are minimal between habitat types. We suggest that these microclimate cues may be poor indicators for selecting a refuge in the spring that will remain suitable terrestrial habitat into the summer, thus salamanders may not rely on microclimate cues to select habitat.

The cues salamanders use to select suitable terrestrial habitat may originate from a variety of sources other than microclimate. Salamanders use olfactory cues in pond sediments to identify "home" ponds (McGregor and Teska 1989), they are primarily fossorial, and they have been shown to select substrates based on pH (Mushinsky 1975). Therefore, we hypothesized that soil and litter may provide reliable cues for terrestrial habitat selection. Our objective was to determine whether juvenile and adult salamanders distinguish between soil and litter collected from a forest and a grassland. We hypothesized that spotted salamanders would select the forest substrate more than the grassland substrate and that selection would be stronger with soil and litter cues combined than with either soil or litter alone.

METHODS

Capture and Handling

We collected 46 adult and 30 juvenile salamanders from ponds located in second-growth, oak–hickory (*Quercus* sp.–*Carya* sp.) forest at the Thomas S. Baskett Wildlife Research and Education Area, Boone County, Missouri, USA. We captured adult salamanders with minnow traps or pitfall traps near the end of the breeding season and during emigration from 4 different ponds. We housed adults in 61 × 92 × 153-cm wood-framed enclosures with fiberglass screen sides at the pond of capture. On 11 April 2002, we moved adult male salamanders into the laboratory and housed them in plastic containers filled with moist leaf litter from the capture site. We used only adult male salamanders in our experiments to eliminate confounding effects of sex. We captured recently metamorphosed (juvenile) individuals on 16 and 21 August and 3 October 2002 in pitfall traps, transferred them directly to 17.5 × 30 × 10-cm plastic containers filled with moist leaf litter from the site of capture, and brought them to a laboratory at the University of Missouri-Columbia. Salamanders were refrigerated at 8–10 °C and removed 6–8 hr prior to experimentation to allow them to acclimate to test temperature (25 °C). All salamanders were released at their site of capture upon the completion of the experiments.

Experimental Design

We performed 4 experiments to examine potential substrate cues used for habitat selection. In 2 separate soil experiments, we presented juveniles and adults with forest and grassland soils. In the litter experiment, we presented adults with forest and grassland litter. Last, we presented adults with a combination of forest soil and litter, and grassland soil and litter.

We collected soil and litter substrates at the Baskett Wildlife Research Area, in the same general area where the salamanders were collected, and at least 50 m from the nearest habitat edge or breeding pond to prevent the collection of substrate from an edge (Murcia 1995). Forest substrate was collected within a mature second-growth, oak–hickory forest. Grassland substrate was collected from grassland consisting primarily of Indian grass (*Sorghastrum nutans*), with some blue stem (*Andropogon gerardii*), and fescue (*Festuca arundinacea*). Historically, the grassland was cultivated until the late 1930s and then left as old field. Warm-season grasses were planted approximately 10 years ago. We collected soil from approximately the top 15 cm and stored it in the laboratory in 10.5-L buckets with lids. We stored litter in plastic bags. We kept soil and litter in the laboratory no more than 3 days prior to an experiment.

In all experiments, the test chamber consisted of a rectangular container (adult test chamber: 50 × 25 × 30 cm; juvenile chamber: 30 × 19 × 11 cm) divided in half width-wise by a piece of plexiglass (2.5-cm high, 0.6-cm thick). We used hardware cloth with open mesh (0.635 cm^2) as the release platform so salamanders were exposed to water loss, thus providing motivation to move to a different location. The release platform also allowed salamanders to simultaneously receive cues from both substrates through the screen. To test for directional biases due to potential homing abilities, the chambers were arranged with half oriented north–south and the other half oriented east–west. In addition, an equal number of forest or grassland substrates were systematically placed in each of the cardinal directions.

Because salamanders normally migrate at night (Semlitsch and Pechmann 1985), we conducted all trials in the dark (with a red light) beginning between 2000 and 2100 hr CST. Ducey and Ritsema (1988) found that salamanders were more active when observed from behind a blind than without a blind; therefore, we stood behind a blind. We observed between 8 and 10 individuals concurrently during each trial. At the start of each trial, we randomly assigned 1 salamander to each chamber. To begin an experiment, we placed a salamander on the release platform, in the center of the chamber, under a cage, with its body oriented perpendicularly to the length of the chamber. After a 5-min acclimation period for juveniles and a 10-min period for adults, we removed the cage and recorded the location of the salamander at 3-min intervals for 1 hr. The location was recorded as "no choice" if all 4 feet were on the release platform. If the salamander had 2 feet on either side of the center divider, the snout position was used to determine the side of choice (as in McGregor and Teska 1989). To control for any cues from conspecifics marking the substrate, soil and litter were used only once and the chamber was scrubbed and dried between trials. We conducted adult tests from 12 to 26 April 2002 and the juvenile tests from 12 November to 4 December 2002. We did not use any salamanders more than once in the same experiment; however, 14 adults were used in another experiment.

Moisture Experiment

To determine whether salamanders behaved in the expected adaptive manner, we tested the responses of 20 juveniles presented with saturated and dry soil collected from the forest. We dried soil in the laboratory on plastic sheets and turned it every other day for 10 days. We saturated half the soil with water (charcoal-filtered and UV-sterilized) and drained it using a double layer of fiberglass screening until rapid dripping stopped. When drying or saturating the soil, we broke clumps and removed large roots or other plant matter. However, the soil was not sifted, thus some small pieces of plant matter may have been present. We placed saturated soil in 1 side of the test chamber and dry soil in the opposing side to the height of the divider (2.5 cm).

Soil Experiments

In 2 experiments, we presented 30 juveniles and 20 adults with a choice between soil collected from the forest and grassland. We saturated both types of soil with the same procedure that we used in the moisture experiment. Saturating the soils with water minimized the temperature and moisture differences between the 2 soil types. We placed forest and grassland soil on opposite sides of the test chamber.

Litter Experiment

We presented 20 adults with a choice between deciduous forest and grassland litter. Because litter does not quickly absorb water when rinsed, we soaked the litter in water (charcoal-filtered and UV-sterilized) in a plastic bag for at least 24 hr until saturated. Before being placed in the test chambers, we rinsed the litter with water and drained with a double layer screen to maintain procedural consistency among experiments. Long pieces of grass were folded or cut and laid in the test chamber. Although this placement of litter does not replicate the vertical structure of grassland, we believe it sufficiently replicates the mat of dead grass found at the base of standing vegetation within a grassland, especially in early spring before new growth emerges.

Combination Experiment

We tested the responses of 20 adult salamanders to a choice between the combination of soil and litter from the forest and the combination of soil and litter from the grassland. We placed a layer of soil in the test chamber following the procedures of the soil experiments. Leaves were placed on top of the forest soil and grass on top of the grassland soil following the procedures of the litter experiment. The 2 layers combined were level with the center divider (2.5 cm). We believe that this experiment most closely repli-

Table 1. Two-tailed binomial test comparing the number of spotted salamanders that selected forest substrate to the number that selected grassland substrate in 4 laboratory experiments. F = number of individuals selecting forest, G = number of individuals selecting grassland, N = no choice, P = sample estimate, and LCL and UCL are lower and upper confidence limits for HO = 0.5.

Experiment	Time interval	F	G	N	P	LCL	UCL	*P*-value
Juvenile soil								
	Throughout the hr	22	3	5	0.88	0.406	0.711	<0.001
	Initial movement	19	7	4	0.73	0.300	0.700	<0.001
	Location at 60 min	21	3	6	0.88	0.291	0.709	<0.001
Adult soil								
	Throughout the hr	14	6	0	0.70	0.272	0.728	0.115
	Initial movement	16	4	0	0.80	0.272	0.728	0.004
	Location at 60 min	10	10	0	0.50	0.272	0.728	0.176
Adult litter								
	Throughout the hr	10	6	4	0.63	0.246	0.748	0.454
	Initial movement	10	6	4	0.63	0.246	0.748	0.454
	Location at 60 min	10	6	4	0.63	0.246	0.748	0.454
Adult combination								
	Throughout the hr	14	6	0	0.70	0.272	0.728	0.115
	Initial movement	12	8	0	0.60	0.272	0.728	0.503
	Location at 60 min	15	5	0	0.75	0.272	0.728	0.041

cates the natural habitat cues that a salamander may encounter because the natural substrate in a given area is composed of both soil and litter.

Data Analysis

For each experiment, we used a 2-tailed binomial test (Zar 1999) to test for forest or grassland preferences at 2 time intervals: (1) initial choice (i.e., direction the salamander left the release platform); and (2) choice at 60 min. Examining the selection at these time intervals indicated whether the salamander detected cues at the release point or gathered cues while searching the chamber. We used a general linear model with a binomial distribution and logit function (SAS Institute 2002) to determine whether the selection of the forest side of the chamber changed with time throughout the hour of observation. We treated individuals as a random effect to account for variation among individuals and identified individuals as subject to treat observations at each 3-min time interval as a repeated measure.

For each experiment, we also used a 2-tailed binomial test to test whether salamanders chose the side of the test chamber with forest or grassland cues more than expected by chance (i.e., 50% forest and 50% grassland), incorporating the choices made throughout the hour of observation. For the 20 observations that occurred during the hour, we classified individuals as choosing either forest or grassland based on the side of the chamber where we recorded >50% of the observations. None of the 60 salamanders tested spent an equal number of observations on each side; therefore, classification was unambiguous.

To examine behavioral differences among the 5 experiments, the number of times an individual crossed the centerline was used as an estimate of movement. We used a single factor analysis of variance (ANOVA) to determine whether the experiment type affected the amount of movement, and we used Tukey pairwise comparisons to compare factor means. To test for directional biases, data from all 5 experiments were combined and salamanders were classified as choosing 1 of the cardinal directions based on the side of the chamber in which >50% of the observations were recorded. We used chi-squared goodness-of-fit test to determine whether a directional bias existed.

RESULTS

In the moisture experiment, juveniles left the release platform toward the saturated side (17 of 19; $P < 0.001$) and selected the saturated side at 60 min (18 of 19; $P < 0.001$). When classifying individuals based on the selection throughout the experiment, 94% selected saturated soil, thus salamanders behaved as expected within the laboratory.

Juvenile and adult salamanders in all experiments tended to select the forest side of the test chamber (Table 1); however, the degree of habitat selection at the 2 time intervals varied among experiments. In the soil experiment, 19 of 26 juveniles initially selected the forest side of the test chamber ($P < 0.001$) and at 60 min, 21 of 24 juveniles selected forest soil ($P < 0.001$). Adults also initially selected the forest soil (16 of 20 adults; $P = 0.004$). However, adults did not select forest soil more than grassland soil at 60 min (10 of 20 adults; $P = 1.000$). In the litter experiment, adults did not select forest litter at either time interval (both $P > 0.05$; Table 1). Adults in the combination experiment did not select forest substrate initially but selected forest substrate at 60 min (15 of 20 adults; $P = 0.041$; Table 1).

We found a larger percentage of juveniles and adults on the forest side of the test chamber in all experiments (Fig. 1); however, the number of adults classified as selecting forest substrate versus the number of adults classified as selecting grassland substrate did not differ (all *P*-values > 0.05, Table 1). In the soil experiments, 5 juveniles made no choice, but the remaining 25 juveniles (88%) were classified as selecting the forest soil ($P < 0.001$). In both the soil experiment and the combination experiment, 70% of adults were classified as selecting the forest. In the litter experiment, 4 adults made no choice; but of the adults that made a choice, 62.5% chose the forest side and 37.5% chose the grassland side.

The selection of forest soil by the juveniles increased with the time of observation ($\beta = 0.210$, SE = 0.055, $P = 0.0008$; Fig. 2), while the selection of forest soil by adults declined throughout the hour of observation ($\beta = -0.209$, SE = 0.035, $P < 0.001$). The selection of the forest side of the test chamber did not change with time when litter was present, as in both the litter experiment ($\beta = -0.140$, SE = 0.097, $P = 0.171$) and the combination experiment ($\beta = 0.097$, SE = 0.049, $P = 0.061$; Fig. 2).

When comparing the activity of salamanders among the 5 experiments (including moisture), experiment type was a significant predictor of the number of times a salamander crossed the centerline (df = 4, mean square error = 1.64, $F = 9.37$, $P < 0.001$). Adult salamanders in the soil experiment moved more than salamanders in the other 4 experiments. No directional biases in adults or juveniles were detected ($P > 0.50$).

DISCUSSION

We concluded from our 4 experiments that salamanders use cues found in the substrate to select forest habitat. We also concluded that salamanders have the ability to select forest habitat without using temperature and moisture cues. The neurophysiological mechanism salamanders use to select substrate types warrants further investigation. Because salamanders migrate at night, olfaction often is hypothesized to be a likely mechanism (McGregor and Teska 1989). In the laboratory, salamanders used olfaction to distinguish between sediment from their home pond and a foreign pond (McGregor and Teska 1989). In a field experiment, salamanders migrated toward a pond; however, orientation changed when the pond was covered with PVC tarpaulin, thereby reducing olfactory cues (Joly and Miaud 1993). The identity of the specific cue within the soil is unknown, but potential olfactory cues may originate from fungi or mycorrhiza, or decomposing vegetation within the forest soil. Habitat selection likely occurs hierarchically through the incorporation of cues received through olfactory, visual, and tactile mechanisms. In addition, habitat selec-

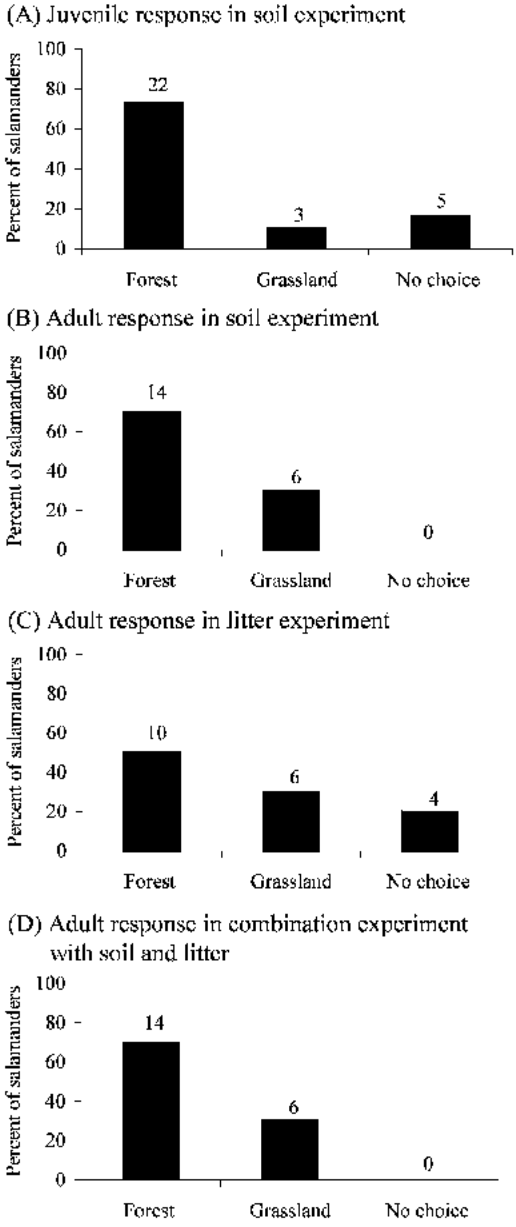

Fig 1. The percent of spotted salamanders that selected forest versus grassland substrate in a laboratory experiment. We classified each individual as selecting forest or grassland based on their selection throughout 60 min of observation. Juvenile (A) and adult (B) salamanders were given a choice between soil collected from a forest or grassland. Adults (C) were given a choice between litter collected from a forest or grassland. Adults (D) were also given a choice between the combination of soil and litter from a forest or grassland. The number of individuals is listed above the bar.

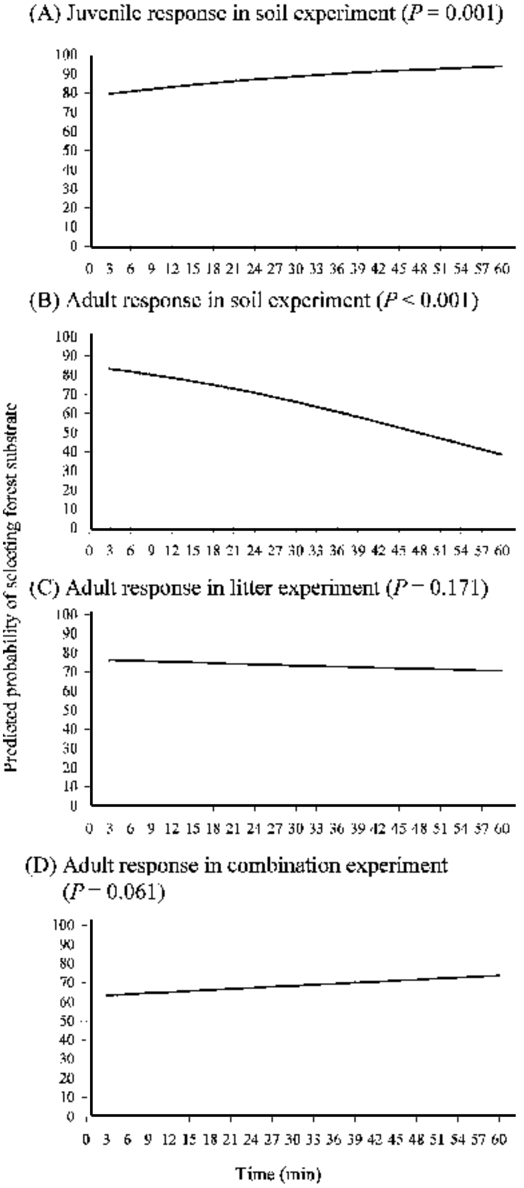

Fig 2. The predicted probability of spotted salamanders selecting forest substrate versus grassland substrate over 60 min of observation in 4 experiments. The probability that an individual chose forest substrate increased through time in the juvenile soil experiment (A), decreased in the adult soil experiment (B), and stayed the same in the adult litter experiment (C) and the adult combination experiment (D). Observations were recorded at 3-min time intervals for 60 min.

tion in natural habitats may occur based on cues received from a variety of sources (e.g., canopy, slope, horizon) in addition to substrate we used in the laboratory. Therefore, the ability of salamanders to select forested habitat under more natural conditions is likely greater than that demonstrated in these simple laboratory experiments.

The choice of forest cues was very clear for juvenile salamanders, with 88% selecting forest soil; whereas 70% of adults were classified as selecting forest soil over grassland soil. The variation in response between juveniles and adults may be attributed to lower physiological tolerances of juveniles. Compared to adults, juveniles have a greater surface area-to-volume ratio, thus desiccation may be a greater threat to juveniles than adults (Spotila 1972). Risk of desiccation may also explain why 94% of juveniles chose saturated substrate and rarely moved from saturated to dry substrates. In addition, emigration of juveniles takes place during the hottest, driest period of the year (i.e., summer; Shoop 1974, Semlitsch 1981). deMaynadier and Hunter (1999) also demonstrated that juvenile spotted salamanders emigrate nonrandomly toward closed-canopy habitat at a greater proportion than adults. Thus, the risk of desiccation, especially within inhospitable grassland habitat (Rothermel and Semlitsch 2002), may provide stronger evolutionary pressure for the selection of moist environments in juveniles relative to adults.

We suggest that adult salamanders initially moved to the forest side of the test chamber based on cues received from the forest soil. Once they reached this side, however, they were unable to find critical elements associated with forest habitat under natural conditions, such as suitable cover (e.g., coarse woody debris, leaf litter). Thus, they explored the test chamber, as indicated by the large number of times that the adult salamanders crossed the centerline. The equal number of individuals on the forest and grassland side of the chamber at 60 min may indicate that they eventually stopped moving at a location independent of soil type.

Adults behaved very differently in the 2 experiments containing litter compared to the soil experiment, further supporting the above explanation regarding cover. When litter was present, we observed salamanders quickly moving under the litter, and they rarely moved between sides of the chamber. Because of the inherent stress animals endure when in the laboratory (Hershey and Forester 1980) and the fossorial nature of salamanders, we suggest that finding cover may have been a primary motivation for salamanders observed in the laboratory.

The forest versus grassland substrate tests, when only litter was present, were not statistically significant. However, the response was always in the same direction, with the largest percentage of individuals choosing the forest leaf litter side of the test chamber. The lack of statistical significance is likely due to the fact that 4 individuals did not make a habitat choice, thus our power to detect an effect was lower in this experiment. A non-choice may have occurred because the salamanders were not receiving strong enough cues from the litter to elicit a response.

We observed the most consistent adult preference for forest substrate in the combination experiment containing both soil and litter. When classifying the individuals in the combination experiment as selecting forest or grassland substrates, 14 (70%) selected the forest substrates and 6 (30%) selected the grassland substrates, but this result was not statistically significant ($P = 0.115$). A result of 15 to 5 would have been significant at $\alpha = 0.05$. A post hoc power analysis showed that a sample size of 30 would have been needed to detect an effect, assuming that 70% is the true proportion of animals selecting the forest substrate. Notably, the percentage of adults selecting the forest substrate in the combination experiment did not decline throughout the hour of observation, as observed in the soil experiment. At any time throughout the hour, between 61.5 and 81.3% of adults were on the forest side of the test chamber. In addition, the number of times the salamanders crossed the centerline in the combination experiment was not significantly different than the litter experiment, indicating they selected the forest soil with litter cover and remained with the choice throughout the experiment. Laboratory experiments, such as these, can add to our understanding of habitat selection by describing the mechanisms underlying movement and behavior observed in the field.

MANAGEMENT IMPLICATIONS

Determining the cues that salamanders use to select habitat increases our ability to prevent potential maladaptive responses to anthropogentic changes in the habitat. For example, under the hypothesis that substrate cues play an important role in habitat selection, a recently harvested forest could become an ecological trap for migrating salamanders. Initially, the soil composition may retain the characteristics of mature forest and thus salamanders may perceive the cues from the substrate as an indication of a favorable environment. Despite the appropriate substrate cues, the open, exposed conditions may pose a threat to the salamanders by reducing survival due to heat and desiccation. In addition, if a forest regeneration project occurs in a highly disturbed area, we hypothesize that the use of this site by salamanders may depend more on the restoration of the forest substrate properties than the growth of trees and formation of canopy cover. The establishment of cues influencing habitat selection provides mechanistic information that could be used to predict habitat selection under scenarios of anthropogenic habitat alteration, such as forest harvest or forest regeneration projects. Knowing the age or stage of regeneration or succession at which forests become suitable for salamanders and at which the salamanders select the forests can facilitate conservation planning. Furthermore, determining the cues influencing habitat selection may be useful for predicting whether an animal will use a corridor, a critical aspect for mitigating forest fragmentation.

ACKNOWLEDGMENTS

We thank F. Thompson and C. Rittenhouse for thoughtful comments on the manuscript. Funding was provided by the University of Missouri-Columbia, Life Sciences Undergraduate Research Opportunity Program, and USGS grant O1CRAG0007 and NSF grant DEB 0239943 to R. D. Semlitsch. Research was conducted under the University of Missouri-Columbia Animal Care and Use Protocol 3368 and the Missouri Department of Conservation collecting permits 11390 and 11140.

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Received 25 June 2003.
Accepted 28 July 2004.
Associate Editor: Gibbs.