An Experimental Investigation of Landscape Resistance of Forest versus Old-Field Habitats to Emigrating Juvenile Amphibians

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Abstract: *We used an experimental approach to investigate the effects of landscape composition on the initial dispersal success of juvenile amphibians. Larval amphibians—spotted salamander (*Ambystoma maculatum*), small-mouthed salamander (*A. texanum*), and American toad (*Bufo americanus*)—were added to artificial pools in four dispersal arrays on forest edges. Each array consisted of a pool surrounded by a circular drift fence with pitfall traps and two 2.5 × 50 m enclosures (runs) extending into forest and old-field habitat. Juveniles captured at the circular fences were individually marked and released into either field or forest runs. We determined initial distance, initial rate, total distance, and net distance moved by juveniles in the field versus forest from recaptures in the runs. We also conducted 24-hour dehydration trials to compare the rates of evaporative water loss by spotted and small-mouthed salamanders in field and forest. Initial orientation of spotted salamanders and toads was significantly biased toward forest. Orientation of small-mouthed salamanders did not differ significantly from random expectations. The avoidance of open-canopy habitat by juvenile American toads in particular indicates that predictions of dispersal behavior based on adult habitat use may be misleading. Spotted salamanders moved almost four times farther and toads more than three times farther into the forest than into the field, and recapture rates of both species were much lower in the field. We attribute the lower recapture rates and shorter distances moved in the field to higher mortality due to desiccation or an abundance of predators. Juvenile spotted and small-mouthed salamanders experienced greater evaporative water loss in the field. Our data on movement behavior and dehydration rates suggest that old-field habitats offer greater landscape resistance to dispersing juveniles of some species. Thus, forest fragmentation is likely to reduce dispersal rates between local populations of these three species, with potentially negative consequences for population persistence in altered landscapes.*

Una Investigación Experimental de la Resistencia de Paisaje de Bosque Versus Hábitats de Campos Viejos sobre Anfibios Juveniles Emigrantes

Resumen: *Utilizamos un enfoque experimental para investigar los efectos de la composición del paisaje sobre el éxito inicial de dispersión de anfibios juveniles. Colcamos larvas de anfibios (salamandras manchadas [*Ambystoma maculatum*] y A. texanum *y sapo americano [*Bufo americanus*]) en estanques artificiales en cuatro secuencias de dispersión en bordes de bosque. Cada secuencia consistió de un estanque rodeado por un cerco circular con trampas de fosa y dos encierros (corridas) de 2.5 × 50 m que se extendían hacia el hábitat de bosque y de campo viejo. Los juveniles capturados en los cercos circulares fueron marcados individualmente y liberados en las corridas de bosque o de campo. A partir de recapturas en las corridas, determinamos la distancia inicial, la tasa inicial, las distancia total y la distancia neta recorrida por juveniles en el campo versus el bosque. También realizamos pruebas de deshidratación de 24 horas para comparar las tasas de pérdida de agua por evaporación en salamandras en el campo y el bosque. La orientación inicial de* Ambystoma maculatum *y* Bufo americanus *estuvo significativamente sesgada hacia el bosque. La orientación inicial de* A. texanum *no fue significativamente diferente de las expectativas aleatorias. La evasión del hábitat abierto en particular por juveniles de sapo americano indica que las predicciones del comportamiento de*

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dispersión basadas en el uso del hábitat por adultos pueden llevar a conclusiones erróneas. Las salamandras manchadas se movieron cuatro veces mas lejos y los sapos más de tres veces más lejos dentro del bosque que dentro del campo, y las tasas de recaptura de ambas especies fueron mucho menores en el campo. Atribuimos las bajas tasas de recaptura y las distancias menores a la mayor mortalidad debido a la desecación o a la abundancia de depredadores. Los juveniles de las dos especies de salamandras experimentaron mayor pérdida de agua por evaporación en los campos. Nuestros datos del comportamiento de movimiento y las tasas de deshidratación sugieren que los hábitats de campo viejo ofrecen mayor resistencia de paisaje para los juveniles dispersantes de algunas especies. Por tanto, es probable que la fragmentación de bosques reduce las tasas de dispersión entre poblaciones locales de estas tres especies, con consecuencias potencialmente negativas para la persistencia de la población en paisajes alterados.

Introduction

Landscape-level studies of amphibian populations in temperate, fragmented landscapes suggest that amphibian occurrence and species richness decline with increased isolation from other wetlands, conversion of land to intensive uses such as agriculture, and higher road densities (Vos & Stumpel 1995; Findlay & Houlahan 1997; Gibbs 1998*a*; Vos & Chardon 1998). Even in relatively undisturbed landscapes, pond-breeding amphibians experience frequent local extinctions and high rates of population turnover (Hecnar & M'Closkey 1996; Semlitsch et al. 1996; Skelly et al. 1999). These observations are consistent with the idea that pond-breeding amphibians exist as metapopulations (Gill 1978; Sjogren 1991; Sinsch 1992) that may decline if habitat fragmentation causes increased rates of local extinction and decreased rates of colonization (Laan & Verboom 1990; Harrison 1991). Many salamanders and anurans that require ponds for breeding and larval development are fully terrestrial as juveniles and adults (e.g., Semlitsch 1998; Lamoureux & Madison 1999). Thus, habitat fragmentation may lead to population declines of amphibians if critical aquatic or terrestrial habitats are destroyed or if remaining patches of suitable habitat become too isolated to allow recolonization by dispersing individuals (Gibbs 1993; Semlitsch & Bodie 1998).

For pond-breeding amphibians, interpond dispersal is the means by which declining populations may be rescued or recolonized following extinction (Brown & Kodric-Brown 1977; Harrison 1991). Because adults rarely switch breeding sites, juveniles are responsible for most instances of interpond dispersal (Gill 1978; Breden 1987; Berven & Grudzien 1990). Despite the potential importance of the juvenile stage for maintaining gene flow and rescuing local populations from extinction, little is known about the factors determining the dispersal ability of juvenile amphibians in different habitats. In a recent study, deMaynadier and Hunter (1999) found that juvenile wood frogs (*Rana sylvatica*) orient toward closed-canopy forest when emigrating from artificial pools at the edge of a power-line right-of-way. Higher temperatures and lower soil moisture in open habitats may be limiting for amphibians, which experience high rates of evaporative water loss (Spight 1968; Spotila 1972) and have poorer dispersal abilities than other vertebrates (Sinsch 1990).

We used an experimental approach to examine the potential effects of landscape composition on the initial dispersal success of three species of amphibians in the midwestern United States. In this region, much of the land surrounding amphibian breeding sites has been converted to cropland or pasture. Such open habitats, which have become the predominant matrix between remaining patches of forest, may be inhospitable to dispersing amphibians. The degree to which different habitats hinder animal movements is an indication of landscape resistance (Ricketts 2001), which may play an important role in determining the response of species to habitat fragmentation. We compared initial movements of juvenile spotted salamanders (*Ambystoma maculatum*), small-mouthed salamanders (*Ambystoma texanum*), and American toads (*Bufo americanus*) emigrating from edges between forest and old-field habitats. Although common in our study area, these three species exhibit divergent habitat associations, leading us to expect differences in their habitat selection and ability to disperse through open habitats.

Methods

Study Site

We conducted our study at the Missouri Department of Conservation's C. W. Green Conservation Area in Boone County, Missouri. This 127-ha research area is a mosaic of second-growth, primarily oak-hickory forest interspersed with open grasslands, idle crop fields, old fields, and small ponds. Our experimental dispersal arrays

were situated on edges between forest and old fields, which are managed with controlled burning on a 5-year rotation. We used edges on relatively flat terrain to avoid the potentially confounding effect of slope.

Experimental Dispersal Arrays

Four replicate dispersal arrays were established on two existing south-facing and two east-facing edges (Fig. 1). Each array was centered on an artificial pool (plastic wading pool 1.5 m in diameter by 36 cm deep) placed in the ground so the rim was level with the soil surface. A drift fence made of plastic-weave silt fencing supported by wooden stakes encircled each pool at a distance of 6 m from the pool's edge. Twelve pitfall traps (no. 10 metal food cans) were placed at approximately 4-m intervals on the inside of the circular fence so that three traps were in the field, three were in the forest, and six were in the intervening habitat classified as edge (similar to study by deMaynadier and Hunter 1999). To prevent mortality due to desiccation or predation, traps contained moist sponges and were shaded by wooden lids held 5 cm above the rim of the can. Two long enclosures (50 × 2.5 m), hereafter referred to as "runs," extended from the circular fence into the forest and field (Fig. 1). Like the circular fence, runs were constructed of silt fencing 60 cm high supported by wooden stakes and buried 12–18 cm in the ground. Pitfall traps with lids were installed at 6.1-m intervals along the inside of the runs. Traps in the runs did not contain sponges, because providing a moist refuge might reverse the effects of dehydration, allowing animals to travel farther than would have been possible under natural conditions.

Several environmental and habitat variables were recorded during the experiment. We measured daily precipitation with a rain gauge at one field run and temperature and soil-moisture with HOBO H8 temperature loggers (Onset Computer Co., Bourne, Massachusetts) and underground soil-moisture sensors (Watermark, Irrometer Co., Riverside, California) installed midway in each run. We

also estimated percent canopy cover and composition of ground cover from measurements taken with an ocular tube at 5-m intervals along each run.

Study Organisms

Spotted and small-mouthed salamanders are 2 of approximately 14 species of mole salamanders (family Ambystomatidae) found in North America. Spotted salamanders are a forest-associated species (Petranka 1998) that may be sensitive to removal of forest, as suggested by their lower abundance within 20 m of forest-clearcut edges compared with interior forest in Maine (deMaynadier & Hunter 1999). Although adults of these two species frequently breed in the same ponds, small-mouthed salamanders may not migrate as far away from breeding ponds as spotted salamanders (Parmelee 1993). Small-mouthed salamanders live and breed in prairies, bottomland forests, and farmlands (Petranka 1998). The ubiquitous American toad occurs in a variety of natural and disturbed habitats and breeds in small, temporary ponds, ditches, or slow-moving streams (Johnson 2000). Like ambystomatids, toads exhibit a high degree of philopatry to their natal pond, although dispersing toads may travel much greater distances than ambystomatids (Oldham 1966; Breden 1987).

We collected multiple egg masses of spotted and small-mouthed salamanders on 1 March and 18 March 2000 from a woodland pond at the Baskett Wildlife Research Area in Boone County, Missouri, approximately 8 km from the C. W. Green Conservation Area. The eggs collected on 1 March were kept outdoors in water tanks (polyethylene cattle tanks; one for each species) at the University of Missouri's Research Park. Egg masses collected on 18 March were refrigerated at 5°C to delay development.

Because there was a limit to the number of animals that could be added to the experimental arrays at any one time, we increased sample sizes by artificially staggering hatching times and subsequent metamorphosis. *Ambystoma texanum* began hatching on 24 March and *A. maculatum* on 2 April. Upon hatching, larvae were transferred to 2000-L cattle tanks containing leaf litter and zooplankton added 3–4 weeks earlier. Each of eight cattle tanks was stocked with 60 *Ambystoma* larvae from the first collection date. The second, smaller group of eggs was removed from refrigeration on 25 April, and the resulting larvae were reared in two additional water tanks. In all, 300 larvae of each species were added to the 10 cattle tanks (5 tanks per species). When larvae reached the developmental stage just preceding metamorphosis (stage 52; Donavan 1980), we transferred them to the artificial pools in the dispersal arrays. We captured *Ambystoma maculatum* metamorphs ($n = 32$) needed for the dehydration experiment with a drift fence at a second pond at the Baskett Area on 12 July, 18 July, and 21 August.
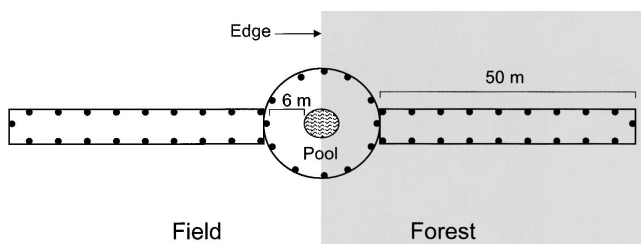

Figure 1. Diagram of an experimental dispersal array showing arrangement of drift fences (black lines) and pitfall traps (small filled circles) used to capture amphibians emigrating from an artificial pool on the field-forest edge.

We collected toad eggs for our study on 23 April and 1 and 10 May 2000 from pools along Hinkson and Grindstone creeks in Boone County, Missouri. Tadpoles were raised in three 1000-L water tanks (approximately 125 tadpoles per tank) containing leaf litter. Tadpoles were fed rabbit-chow pellets every few days. We transferred tadpoles to the artificial pools in the dispersal arrays at an advanced developmental stage (stages 37–41; Gosner 1960).

Experiments

INITIAL ORIENTATION

Artificial pools were filled and stocked with leaf litter and zooplankton 3 weeks before larvae were added. Fiberglass window screening was attached to the rim of each pool to facilitate emigration by metamorphic amphibians. Between 29 May and 21 July, small groups of late-stage *Ambystoma* larvae and *Bufo* tadpoles were added to the pools in the dispersal arrays. Salamanders were added on 29 May ($n = 20$ of each species to each pool), 16 June ($n = 9$), 11 July ($n = 7$), and 21 July ($n = 3$). Toads were added on 2 June ($n = 24$ to each pool), 5 June ($n = 10$), 19 June ($n = 10$), and 27 June ($n = 20$). Individual larvae were haphazardly assigned to groups, and groups of larvae were randomly assigned to one of the four pools. By adding more than one species at a time to the experimental arrays, we potentially violated the assumption of independence among species in their emigration behavior. We chose this approach because we had limited resources with which to construct the arrays and because these three species naturally co-occur in ponds in our area. In addition, although the possibility of interspecific interactions during emigration exists, we are not aware of any studies documenting such effects.

We determined initial orientation—initial direction of movement with respect to habitat type—by checking and recording captures in pitfall traps at the circular fences every morning (0830–1130 hours). Each captured individual was measured, given a unique toe-clip, and released immediately just inside one of the runs. Juveniles captured in the three forest traps were released into the forest run, and those captured in field traps were released into the field run. Juveniles captured in the six edge traps were randomly assigned to a run by a coin toss. This procedure ensured sufficient sample size in both runs, in the event that juveniles demonstrated an extreme habitat preference, and was justified because our primary interest was in the behavior of dispersers in forest and field habitats. Log-likelihood ratio *G* tests (Sokal & Rohlf 1995) were used to determine whether emigrating metamorphs oriented randomly with respect to habitat type. Because of low capture rates of some species at some sites, we conducted a *G* test for each species with data pooled across sites and dropped the edge category. Thus, if orientation were random, we would expect an equal proportion of captures in forest and field traps.

EMIGRATION

We checked pitfall traps in the runs daily between 0830 and 1130 CST. Captured individuals were identified, measured, and released back into the center of the run next to the point of capture. The first recapture of each individual was used to determine initial distance and initial rate of emigration (initial distance/number of days since release into run). Initial rate could not be calculated for 57 juveniles (26 spotted salamanders, 4 small-mouthed salamanders, and 27 toads) that managed to bypass the circular fence and were captured for the first time in one of the runs, but the initial, total, and net distances moved by these originally unmarked individuals were included in the analyses. Total distance and net distance were calculated only for juveniles recaptured more than one time in the runs. Because only one small-mouthed salamander was recaptured more than once, we could not calculate total and net distance for this species. Total and net distance were based only on movements to and away from the pools, because we documented only two instances of side-to-side movements within a run. Experimental animals were removed from runs upon their third recapture or upon capture at the end (50 m) of each run. We also recorded numbers of snakes, lizards, shrews, and rodents captured or observed in the runs.

We used multivariate analysis of variance (MANOVA), which takes into account collinearity among response variables, to test for the effects of habitat (forest vs. field), species, and their interaction on three response variables: initial, total, and net distance (PROC GLM; SAS Institute 1989). Several of the response variables related to emigration behavior were significantly correlated (initial distance and initial rate: Pearson's $r = 0.4184$, $p = 0.0526$, $n = 22$; initial and total distance: $r = 0.6240$, $p = 0.0001$, $n = 39$; total and net distance: $r = 0.3598$, $p = 0.0245$, $n = 39$). We also examined the effects of habitat, species, and their interaction on initial rate and initial, total, and net distance separately using univariate analyses of variance (ANOVA) (PROC GLM; SAS Institute 1989). Our statistical analyses were based on the mean values obtained for each species in each run. Each run was a true replicate, whereas using individual-based data in analyses could have been considered pseudoreplication because of the possibility of nonindependence among individuals within the same run (Hurlbert 1984). Due to unequal sample sizes, all *F* values were calculated with Type III sums of squares.

DEHYDRATION

To compare rates of evaporative water loss of salamander metamorphs in forest versus field habitats, we
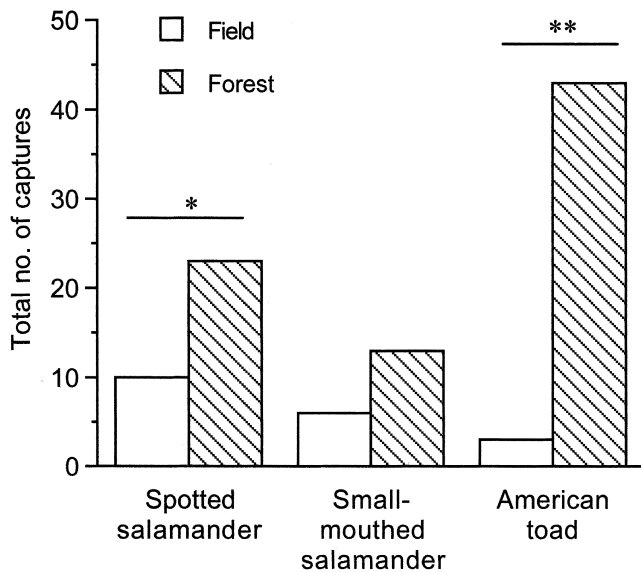
*Figure 2. Initial orientation with respect to habitat type (total number of captures at circular fences) for three species of amphibians emigrating from pools on forest edges. Asterisks indicate significant differences based on log-likelihood ratio G tests (*p < 0.05; **p < 0.001).*

Table 1. Results of multivariate analysis of variance of the effects of habitat, species, and their interaction on initial dispersal success, based on distances moved by juvenile amphibians captured more than once in the runs.*

Source of variation	df	Wilks' λ	F	p
Habitat	3,6	0.0951	19.04	0.0018
Species	6,12	0.2654	1.88	0.1653
Habitat × species	3,6	0.1002	17.96	0.0021

*Small-mouthed salamanders were excluded from the analysis because only one individual of this species was recaptured more than once.

ted salamander from the third trial were deleted from the analyses because the animal was kept in captivity longer than other subjects, appeared to be in poor condition, and suffered unusually high weight loss during the first 8 hours. At each weighing, we recorded relative humidity (HOBO RH logger) in the run and soil temperature (Aquaterr Moisture Meter, Aquaterr Instruments, Costa Mesa, California) in each cage. We used repeated-measures analysis of covariance (ANCOVA), with initial mass as the covariate, to test for the effects of trial, array, habitat, species, and their interactions on the measurements of proportional water loss (weight loss/initial mass) for each individual (PROC GLM; SAS Institute 1989).

conducted three dehydration trials in the runs. Two small cages were installed at the midway point (25 m) in each run. To construct each cage, we removed both ends of a number 10 can and inserted it vertically into the ground, leaving 3 cm of the can showing above ground. A cylindrical mesh top made of aluminum window screening was attached to the rim of the can and held closed by binder clips. The soil and ground cover were minimally disturbed during installation of the cages, which proved effective in confining metamorphs while still providing them with a realistic microhabitat.

Postmetamorphic small-mouthed salamanders from our cattle tanks and spotted salamanders from the Baskett Area were held in the laboratory at room temperature in plastic containers with moist leaf litter for no more than 4 days prior to trials. The evening before a trial, salamanders were transferred to individual plastic containers with 1 cm of aged tap water. In the morning, they were weighed to obtain their fully hydrated initial mass and then transferred to individual cages in the field. In the first two trials, we tested one individual of each species in each run (*n* = 4 in each habitat type). We did not have enough small-mouthed salamanders for the third trial, so we ran the trial with two spotted salamanders in each run. Salamanders were weighed in the field after 8–9 hours, returned to the cages, and reweighed after 22–25 hours. Any weight loss observed during this short time was assumed to be due to water loss (Pough & Wilson 1970). Measurements of one spot-
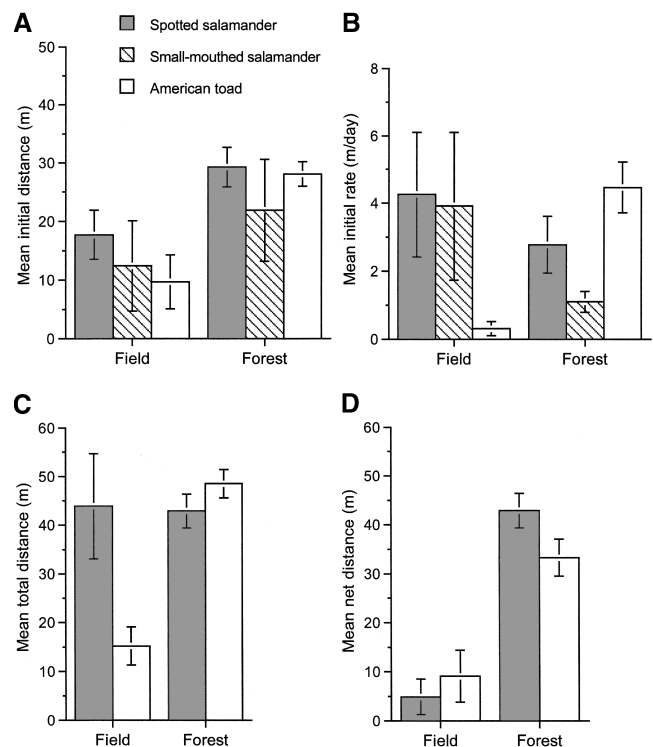

Figure 3. Mean (a) initial distance, (b) initial rate, (c) total distance, and (d) net distance moved by juvenile amphibians emigrating in field and forest runs. Lines within bars represent standard errors.

Results

Initial Orientation

Of the larvae added to pools, an average of 41.0% of the spotted salamanders, 16.5% of the small-mouthed salamanders, and 32.4% of the American toads were captured at the circular fences. Whereas spotted salamanders and toads exhibited nonrandom orientation biased toward the forest ($G = 5.26$, df = 1, $p < 0.025$; $G = 41.59$, df = 1, $p < 0.001$; respectively by species), captures of small-mouthed salamanders did not differ significantly from random expectations ($G = 2.64$, df = 1, $p > 0.10$; Fig. 2). Although edge captures were not included in the G tests, they accounted for 48% of captures of the spotted salamander, 42% of the small-mouthed salamander captures, and 45% of the toad captures at the circular fences. The expected proportion of edge captures, assuming random emigration, was 50%.

Emigration

Of the 179 emigrating juveniles marked and released into the runs, 70 were recaptured at least once. Average recapture rates of marked spotted salamanders and toads were higher in the forest runs (33.3% and 73.1%, respectively) than in the field runs (16.7% and 27.5%, respectively). Average recapture rates for small-mouthed salamanders were similar in forest (20.0%) and field (23.1%) runs.

Initial dispersal success, as measured by the multivariate response of emigrating juveniles, was significantly affected by habitat type (Table 1). There was also a significant interaction between habitat and species in the MANOVA (Table 1). On average, individuals of all three species traveled farther initially in the forest than in the field (Fig. 3a), resulting in a significant effect of habitat on initial distance in the univariate ANOVA (habitat: $F_{1,14} = 5.14$; $p = 0.0398$; species: $F_{2,14} = 0.62$, $p = 0.5537$; habitat $\times$ species: $F_{2,14} = 0.62$, $p = 0.5538$). Initial rate, however, did not vary significantly according to habitat or species (habitat: $F_{1,12} = 2.32$, $p = 0.1534$; species: $F_{2,12} = 1.83$, $p = 0.2020$; habitat $\times$ species: $F_{2,12} = 0.88$, $p = 0.4395$; Fig. 3b).

Although the mean total distance moved by spotted salamanders was similar in the forest and field (Fig. 3c), four of the five individuals in the field made out-and-back movements in which they ventured down the run initially but then reversed direction and were recaptured at the starting point. In the study as a whole, four spotted and two small-mouthed salamanders made out-and-back movements in the field, whereas none did in the forest. In contrast, five toads made out-and-back movements in the forest and none did in the field, but a significant number of toads still reached the end of runs in the forest ($n = 23$). Together, these observations contrib-
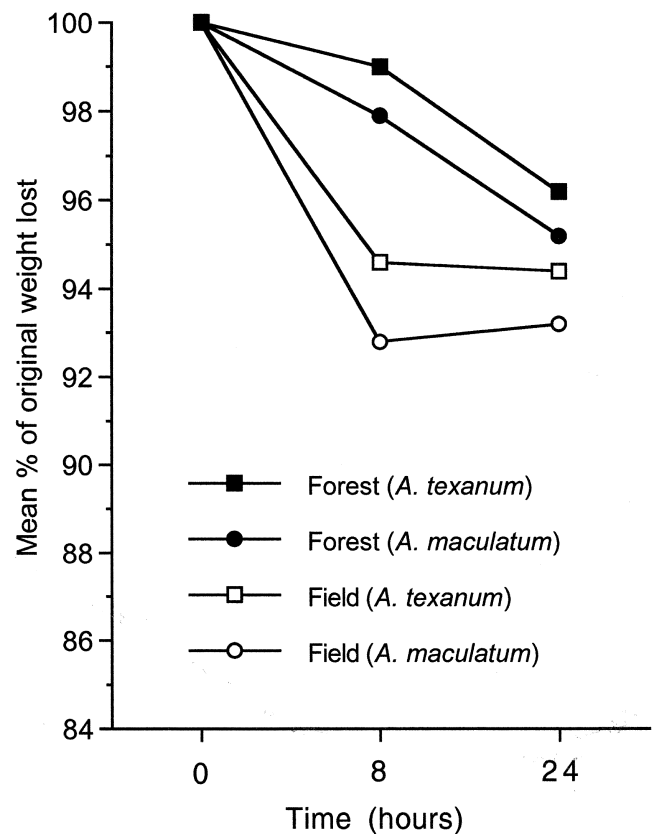
uted to a significant interaction between habitat and species in the univariate ANOVA for total distance and in the MANOVA. The ANOVA of total distance revealed significant effects due to habitat ($F_{1,8} = 16.76$, $p = 0.0035$), species ($F_{2,8} = 6.33$, $p = 0.0225$), and habitat $\times$ species ($F_{1,8} = 22.45$, $p = 0.0015$). Mean net distances moved by spotted salamanders and toads were consistently higher in the forest than the field (Fig. 3d), resulting in a significant effect of habitat in the univariate ANOVA (habitat: $F_{1,8} = 70.61$, $p = 0.0001$; species: $F_{2,8} = 0.37$, $p = 0.7035$; habitat $\times$ species: $F_{1,8} = 3.03$, $p = 0.1200$).

Vegetation in the field runs comprised, on average, 40% grasses and 60% other herbaceous plants, with an average height of 58 cm. In the forest runs, tree-canopy cover averaged 88% and the ground cover comprised 53% leaf litter, 30% woody shrubs (<1.5 m tall), 17% grasses and other herbaceous plants, and $<1\%$ each of woody debris and bare soil. Average daily soil moisture was generally higher in the field runs (7.5 centibars in June, 19.0 in July, and 11.6 in August; saturated soils measure 0–10 centibars) than in the forest runs (13.8 in June, 39.4 in July, and 23.8 in August). Average daily temperatures tended to be higher in the field than in the

Figure 4. Mean percentage of original weight lost over 24 hours by juvenile spotted and small-mouthed salamanders in three dehydration trials.

Table 2.   Mean initial mass and snout-vent length (SVL) of juvenile salamanders in the three dehydration trials.*

Trial	Species	n	Mean initial mass (g)	Mean SVL (mm)	Mass-to-length ratio
1	A. maculatum	8	1.00	30.0	0.033
	A. texanum	8	0.77	30.9	0.025
2	A. maculatum	8	0.89	29.0	0.031
	A. texanum	8	0.70	29.8	0.023
3	A. maculatum	15	1.13	31.6	0.036

*SVL is the head-body length measured from the tip of the snout to the posterior end of the cloaca.

forest runs. In particular, fields experienced average daily maximum temperatures of 36.2° C in June, 41.4° C in July and 42.1° C in August. These maximum field temperatures were 9.7° C, 12.4° C, and 11.9° C higher than the corresponding maximum temperatures in the forest.

Dehydration

Trial, array, and habitat were significant between-subject effects in the repeated-measures ANCOVA of water loss (trial: $F_{2,6} = 6.65$, $p = 0.0301$; array: $F_{3,6} = 13.90$, $p = 0.0041$; habitat: $F_{1,6} = 29.80$, $p = 0.0016$; Fig. 4). Despite the slightly smaller mass-to-length ratio of small-mouthed salamanders (Table 2), there was no significant effect of species ($F_{1,6} = 0.00$, $p = 0.9697$). This held true even when the covariate, initial mass, was dropped from the model (species: $F_{1,7} = 2.74$, $p = 0.1420$). The only significant within-subject effect in the repeated-measures ANCOVA was a time-by-habitat interaction (Wilks' λ = 0.5002, $F_{1,6} = 6.00$, $p = 0.0499$). Water loss occurred more rapidly in the field than in the forest (Fig. 4). During the dehydration trials, mean above-ground maximum temperature in the field and forest runs was 39.9° C and 28.3° C, respectively. Mean soil temperature, measured 8 hours into each trial, was similar in the field (26.7° C) and forest (25.7° C). Mean relative humidity was also similar in the field (79.8%) and forest (80.8%).

Discussion

Our experimental results suggest that forest fragmentation may hinder initial dispersal of some amphibian species. As observed by deMaynadier and Hunter (1999) for juvenile wood frogs, we found that spotted salamander and American toad metamorphs also significantly avoided open-canopy habitats upon leaving the pools. We captured twice as many small-mouthed salamanders entering forest, but the difference in orientation was not statistically significant. Our ability to detect a difference

may have been compromised by the low number of captures of small-mouthed salamanders at the circular fences. Small-mouthed salamanders may have experienced higher mortality in the pools or exhibited different behaviors that reduced the probability of capture with drift fences. Juvenile spotted and small-mouthed salamanders experienced comparable dehydration rates, despite a difference in body shape between the two species. We expected small-mouthed salamanders to experience greater water loss because, other things being equal, evaporative water loss increases with increasing ratio of surface area to volume (Spight 1968). Our measurements may not have been precise enough to detect small differences in weight loss, or perhaps small-mouthed salamanders possess physiological or behavioral adaptations for minimizing water loss (e.g., coiling, aggregating; Spotila 1972).

Toad metamorphs overwhelmingly selected forest habitat. Only 3 of 83 emigrating toads were captured along the field section of the circular fences. Compared with salamanders, anurans are typically more tolerant of hot, dry conditions (Duellman & Trueb 1986). American toads have also remained abundant in some agricultural areas (Kolozsvary & Swihart 1999), so we assumed that they would be less sensitive to factors such as canopy cover. Toad metamorphs, however, may lack physiological tolerance to desiccation stress because of their small size (average snout-vent length in our study was 14.9 mm ± 4.1 SD). Taigen and Pough (1981) suggested that American toads do not disperse until they reach approximately 0.3–0.4 g, at which point their capacity for aerobic metabolism is sufficient to allow sustained activity. Most of the toads captured at our circular fences were smaller than this threshold size, suggesting that the cooler conditions in the forest provided an opportunity for them to initiate dispersal and foraging earlier than might have been possible if the pools were located in open habitats. In addition, juvenile toads may prefer forest for other reasons, such as the availability of food resources or cover. Our results imply that knowledge of adult habitat use may be a poor basis for predicting the behavior of dispersing juveniles.

The responses of juveniles placed in the runs provided more definitive information on how habitat type might influence dispersal success. Recapture rates of spotted salamanders and American toads marked and released into runs were approximately twice as high in the forest as in the field. Recapture rate of small-mouthed salamanders was similar in both habitats, but the small number of small-mouthed salamanders recaptured does not provide a reliable basis for conclusions about this species' response. Movements of all three species were significantly farther in the forest than in the field. The difference was even more striking when we compared net distances, thus correcting for any reversals in direction. On average, spotted salamanders moved almost four

times farther and toads more than three times farther into the forest. No toads ever reached the end of the field runs, whereas 23 were captured at the end of forest runs. Net distances thus provided a measure of the degree to which each habitat type was resistant to, or filtered, dispersing individuals. We did not detect differences in initial rate between habitat types or among species, perhaps because our methods did not allow continuous observations of movement. Rate of travel by amphibians also varies greatly according to weather, especially rainfall.

Juvenile amphibians in the field may have suffered higher mortality due to desiccation or an abundance of predators, especially snakes. We recorded 12 snakes during the course of the experiment, including four garter or ribbon snakes (*Thamnophis* spp.), which are known to prey on amphibians (Johnson 2000) and which were seen only in field habitats. Juvenile salamanders experienced significantly greater water loss in the field than in the forest, and dehydration occurred more quickly in the field. In addition, the average daily maximum temperatures in the field in July and August exceeded by approximately 2° C the critical thermal maximum for juvenile spotted salamanders (39.7° C; Pough & Wilson 1970). The out-and-back movements by six juvenile salamanders placed in field runs suggest that reversals, rather than continued travel in the same direction, are indicative of juvenile ambystomatids attempting to escape unfavorable conditions.

We interpret the out-and-back movements by five juvenile toads in forest runs differently from those made by salamanders. Because toads moved more frequently and more independently of rainfall than the salamanders, their out-and-back movements may have resulted from the artificially confining nature of the runs. In addition, many more toads reached the end of runs in the forest than returned to the starting point. If the forest were unsuitable habitat, we would have expected more toads to have reversed direction toward the fields, and at least some captures at the end of the field runs. These observations imply that inherent differences in movement behavior between anurans and caudates may need to be considered when experimental studies are designed and interpreted.

If dispersing juvenile amphibians tended to move less in favorable habitats, as observed for butterflies (Haddad 1999) and a plethodontid salamander (Rosenberg et al. 1998), then lower recapture rates and shorter movement distances in the field could be explained by juveniles settling into small activity centers (as observed by Semlitsch 1981). By this reasoning, the fields were suitable habitat and we might have eventually recaptured these animals if we had run the experiment longer. We think this is unlikely, because most toads (88%) had been marked and released by 20 July, and we continued to monitor arrays for 5 more weeks. Oldham (1985)

found that dispersing juvenile toads moved at a rate of approximately 1.5 m/day in thick grassy scrub. Even if our toads moved at this slow rate, they would have encountered our fences and pitfall traps frequently. In addition, the 20 days with measurable rainfall during our study provided favorable conditions for movement. Thus, we suggest that juvenile toads and salamanders actually experienced higher mortality in the fields.

Conservation Implications

Amphibian diversity in both industrialized and nonindustrialized regions of the world is declining due to habitat loss and alteration (Blaustein et al. 1994; Alford & Richards 1999). Because of their complex life cycles, limited mobility, and high degree of philopatry, amphibians may be particularly sensitive to habitat alteration caused by urban development or agricultural and forest management practices (Blaustein 1994; deMaynadier & Hunter 1995). The behavioral responses we observed indicate that juvenile amphibians are capable of perceiving, and may preferentially use, remnant patches of suitable habitat and movement corridors. Instead of juveniles emigrating randomly from ponds in fragmented landscapes, which could result in "demographic drain" (Gibbs 1998*b*), our findings demonstrate that juvenile amphibians are capable of detecting and avoiding unfavorable habitat.

By comparing the movement behavior of juvenile amphibians between habitat types and among species, we gained information on individual-level responses to landscape structure that may contribute to population-level responses of amphibians to forest fragmentation. The behavioral avoidance and possibly higher mortality rates of juveniles in the fields in our study imply that habitat fragmentation is likely to reduce dispersal rates between local populations of these three species. Finally, results from studies like ours are needed for further development of spatially explicit models of amphibian population dynamics (Halley et al. 1996) and could aid in the development of movement models similar to those derived for other taxa (e.g., Haddad 1999; Jonsen & Taylor 2000).

Acknowledgments

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