Ecological Applications, 14(5), 2004, pp. 1535–1546

MIGRATORY SUCCESS OF JUVENILES: A POTENTIAL CONSTRAINT ON CONNECTIVITY FOR POND-BREEDING AMPHIBIANS

BETSIE B. ROTHERMEL[1]

Division of Biological Sciences, University of Missouri, 105 Tucker Hall, Columbia, Missouri 65211-7400 USA

Abstract. The persistence of pond-breeding amphibians in highly fragmented landscapes may be constrained by the need for connectivity between aquatic breeding sites and suitable terrestrial habitat, an example of landscape complementation. Although migratory ability determines the spatial scale at which landscape complementation operates, the factors influencing migratory success of amphibians, especially of juveniles, are poorly understood. This study is the first to investigate whether juvenile amphibians possess any innate, long-distance orientation mechanisms that might improve their chances of locating suitable terrestrial habitat. I conducted experimental releases of spotted salamanders (*Ambystoma maculatum*) and American toads (*Bufo americanus*) from 18 artificial pools in replicate pastures at distances of 5–50 m from the nearest forest edges. Using circular drift fences with pitfall traps, I captured, individually marked, and released metamorphosed salamanders ($n = 323$) and toads ($n = 203$) leaving each pool. Salamanders exhibited nonrandom orientation at nine pools, but at only one was the mean movement direction consistent with the direction to the nearest forest edge. Emigrating salamanders probably responded to microtopographic or other distinct features of each pool, rather than to distant cues. Migratory success was determined by recaptures of marked juveniles at drift fences along the forest edges. I used logistic regression to model probability of recapture and evaluated alternative models using an information-theoretic approach. Migratory success of both species was primarily a function of distance to nearest forest. Of salamanders and toads released from 50-m pools, <15% reached the forest, suggesting that few juvenile amphibians would be able to migrate greater distances across pastures. Breeding sites lacking connectivity to suitable terrestrial habitat may be population sinks due to high mortality of juveniles during emigration. Additional research is needed to determine appropriate threshold distances between breeding sites and terrestrial habitat, as well as the potential effectiveness of movement corridors for migrating amphibians.

Key words: Ambystoma maculatum; *American toad;* Bufo americanus; *connectivity; dispersal; juvenile amphibians; landscape complementation; mark–recapture; migration; orientation; perceptual range; spotted salamander.*

INTRODUCTION

Dispersal ability and movement behavior are critical factors determining the persistence of a species in the face of habitat loss and fragmentation. As patches of suitable habitat become increasingly isolated, interpatch dispersal and colonization rates are influenced by an animal's willingness to leave patches of suitable habitat and its efficiency in locating new habitat patches. These aspects of movement behavior have not been investigated directly for pond-breeding amphibians, a group of small vertebrates that may be especially vulnerable to habitat alteration. Even in the absence of anthropogenic disturbance, local populations of pond-breeding amphibians experience high rates of extinction due to drought and other factors (Semlitsch et al. 1996, Skelly et al. 1999, Marsh and Trenham 2001). Their persistence at a landscape level, therefore, may depend on maintaining dispersal rates to allow for recolonization, as occurs in metapopulations (Semlitsch 2000, Marsh and Trenham 2001).

At the scale of local populations, persistence also depends on maintaining migratory links between critical habitat elements. Pond-breeding frogs, toads, and salamanders require different habitats at different stages of their life cycle and have relatively limited mobility (Sinsch 1990). Joly et al. (2001) found that the abundance of newts (*Triturus* spp.) was positively correlated with the width of the noncultivated sector linking ponds to available forest within a 400 m radius of the pond. In a study of leopard frogs (*Rana pipiens*) in a heterogeneous landscape near Ottawa, Canada, Pope et al. (2000) found that information on both the amount of summer habitat and density of breeding sites was required to model the distribution and abundance of this species. Both studies support the role of landscape complementation (Dunning et al. 1992) in determining the distribution and persistence of amphibian populations in fragmented landscapes. In this context,

Manuscript received 30 June 2003; revised 23 December 2003; accepted 4 February 2004. Corresponding Editor: R. D. Semlitsch.

[1] Present address: Savannah River Ecology Lab, Drawer E, Aiken, South Carolina 29802-1030 USA.
E-mail: rothermel@srel.edu

landscape complementation refers to the need for maintaining connectivity between aquatic breeding sites and terrestrial habitat.

Like ranid frogs, salamanders in the family Ambystomatidae and toads in the family Bufonidae require different habitats during the breeding and nonbreeding season. Although small wetlands are required for breeding, adults and postmetamorphic juveniles live a largely terrestrial existence, occupying nonbreeding home ranges at some distance from aquatic sites (centered on burrows, in the case of salamanders; Oldham 1966, Semlitsch 1981, 1998). In undisturbed habitats, adult ambystomatid salamanders may migrate up to 625 m from ponds (mean 125 m), and juveniles considerably less (Semlitsch 1998). Adult bufonids may migrate >1 km from ponds (range 23–1600 m; Semlitsch and Bodie 2003).

In landscapes undergoing habitat fragmentation, the terrestrial habitat surrounding breeding sites is often converted to agriculture or other intensive land uses. Open habitats are relatively impermeable to adult spotted salamanders (*Ambystoma maculatum*; Whitford and Vinegar 1966, Rittenhouse 2002), although they sometimes traverse nonforested land to reach breeding sites (Shoop 1965, Gibbs 1998; *personal observation*). These same habitats may be substantial barriers for small juveniles because of harsh environmental conditions, behavioral avoidance, or both. For example, juvenile spotted salamanders and American toads (*Bufo americanus*) emigrating from artificial pools on forest edges oriented nonrandomly, avoiding old fields and emigrating toward forest (Rothermel and Semlitsch 2002). In a similar experiment, juvenile wood frogs (*Rana sylvatica*) avoided the open habitat under powerline rights-of-way (deMaynadier and Hunter 1999). Unlike adults, juveniles are inexperienced with the terrain and may not be able to determine the shortest route from their pond to terrestrial refuges. Their small body size also puts them at higher risk of desiccation, which may be a major cause of natural mortality in recently metamorphosed salamanders (Pough and Wilson 1970, Shoop 1974, Semlitsch 1981).

Zollner (2000) showed how the perceptual ability of three species of forest-dwelling sciurids was inversely related to their sensitivity to habitat fragmentation. The species able to detect preferred habitat from the farthest distance was also the species that tended to persist longest in landscapes undergoing fragmentation. Zollner (2000) also suggested that perceptual ability could be related to differences in body size and that juveniles might have more limited perceptual ranges than adults. Because of the potential differences between adults and juveniles, the factors influencing migratory success of both life stages need to be considered when assessing the spatial scale at which landscape complementation might be important for amphibians. An important question is whether migrating juveniles possess any innate, long-distance orientation mechanisms that might improve their chances of locating suitable terrestrial habitat, especially in fragmented landscapes. The ability of amphibians to home toward their pond of origin is well documented (Sinsch 1990) and has been linked to the use of olfactory cues (McGregor and Teska 1989, Joly and Miaud 1993), but their perceptual abilities in relation to terrestrial habitat characteristics have not been examined experimentally.

I examined these aspects of movement behavior by conducting experimental releases of juvenile spotted salamanders and American toads from artificial pools in replicate pastures adjacent to forest. My primary objective was to determine whether emigrating juveniles exhibit target-oriented movement toward forest habitat that would be suggestive of some long-distance perceptual ability. Target-oriented movement would be expressed as a directional movement path (Sjogren-Gulve 1998) and would require both a long-distance environmental cue to provide directional information and the ability to perceive that cue. By placing pools in fields at different distances and cardinal directions from forest, I tested whether emigrating juveniles oriented toward the closest forest and whether such behavior was influenced by proximity to forest. One prediction was that, if juvenile amphibians possess limited perceptual range (i.e., can only detect landscape elements at short distances; Lima and Zollner 1996), then they would be less likely to exhibit target-oriented movement at pools located greater distances from forest. Finally, I used mark–recapture techniques to examine how distance and other factors influenced the probability of juveniles reaching the forest.

METHODS

Experimental arrays

In May 2001, I installed artificial pools in two pastures in the Mark Twain National Forest, Boone County, Missouri, USA (Fig. 1). The pastures were dominated by fescue, a non-native grass. They had been grazed by cattle in the recent past, but no livestock were present during this study. Eighteen 1.5 m diameter plastic wading pools (nine in each pasture) were placed in the ground at four approximate distances from the nearest forest edge ($n = 3$ at 5 m, $n = 5$ each at 10, 25, and 50 m). The direction to the nearest forest varied among pools within each distance category, thus controlling for any inherent bias in movement direction of emigrating amphibians. Pools were filled with water, then stocked with leaf litter and zooplankton obtained from forested ponds 3–4 km away.

Each pool was encircled by plastic silt fencing 4 m from the pool's edge. Eight evenly spaced pitfall traps (metal cans) were installed along the inside of each pool fence. Traps contained moist sponges and were shaded by wooden lids held 5 cm above the rim of the can. Drift fences were also installed along the three forest edges bordering each field (Fig. 1). Like the pool

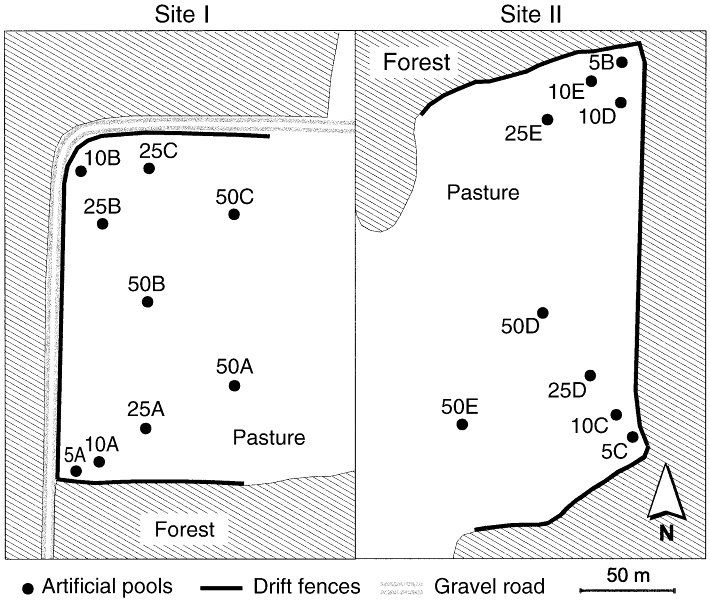

FIG. 1. Spatial arrangement of the 18 artificial pools and edge drift fences in the two pastures used in the study. Pools were placed at minimum distances of 5, 10, 25, and 50 m from neighboring forest edges.

fences, the edge fences were made of silt fencing buried 12–18 cm in the ground. Pitfall traps were installed every 8 m along the edge fences.

Amphibian releases

2001.—I collected ~20 spotted salamander egg masses in mid-March from a woodland pond located 3.1 km south-southwest of the pastures where releases were conducted. Larvae were raised in cattle tanks at an outdoor facility at the University of Missouri, which is located 24 km north-northwest of the study site. I head-started larvae in cattle tanks rather than adding them to the pools immediately, because cattle tanks provided a relatively low-density and predator-free environment, ensuring larger sizes at metamorphosis and higher larval survival. Salamander larvae were transferred to pools in the pastures when they reached the final stage of development preceding metamorphosis (i.e., stage 52 just before gill absorption; Donavan 1980). Between 29 May and 7 July, I added multiple batches of larvae to the pools until each pool had been stocked with 49–55 larvae.

In mid-May, I collected American toad eggs from several clutches found in a flooded agricultural field in the Missouri River floodplain near Easley, Missouri, ~17 km west of the study site. Like salamander larvae, toad tadpoles were raised in cattle tanks at the University of Missouri and were transferred to pools in the pastures when they reached the final stages of larval development (Stages 37–41; Gosner 1960). Between 17 June and 20 July, I added multiple batches of tadpoles to the pools until each had been stocked with 60–63 tadpoles. For both salamanders and toads, the larvae raised in different cattle tanks were mixed and groups of larvae were haphazardly assigned to pools.

I checked pitfall traps around pools for metamorphosed amphibians every morning from 5 June to 14 September 2001. Juveniles captured emigrating from the pools were measured and given individual marks by toe-clipping, and were then released outside the pool fence. Pitfall traps along the forest edge were checked daily after the first juveniles were released. Juveniles recaptured at the forest edge were identified according to pool and were removed from the experiment. The experiment was terminated when there were no new captures for 20 days. To confirm that juvenile amphibians did not overwinter in the fields, I reopened the forest edge traps periodically in March, April, June, July, and August of 2002 for a total of 78 nights. Although I captured several adult spotted salamanders from the site's existing population, I did not capture any juvenile salamanders or toads previously marked in 2001.

2002.—Because toad survival was low in the first year, I partially replicated the study in the following year by releasing toad tadpoles into 12 pools, including three in each distance class (all nine pools at Site II and pools 5A, 25A, and 50C at Site I; Fig. 1). I collected American toad eggs from three different clutches in a pool along Hinkson Creek, Boone County, Missouri, on 15 April. As before, I raised toad tadpoles in cattle tanks and then transferred 48–51 tadpoles to each pool in late May, when they had reached developmental stages 36–38 (Gosner 1960).

I also increased sample sizes for spotted salamanders by replicating releases of this species at a subset of the pools (5-m pools 5A, 5B, and 5C and 25-m pools 25A, 25D, and 25E; Fig. 1). I collected portions of eight spotted salamander egg masses in early April from the same pond as in 2001 and raised the larvae as before, transferring them to pools in the pastures when they reached stage 52 (Donavan 1980). I added 26–27 salamanders to each of the six pools in mid-June.

I checked the traps along the pool drift fences every morning beginning on 29 May 2002. The first metamorphosed toads were captured on 31 May, seven days after the first toad tadpoles were added to the pools. The first salamander was captured on 19 June, eight days after the first salamander larvae were added to the pools. I closed traps at the pools on 25 July, because no toads and only one salamander had been captured in the preceding 10 days. In 2002, I toe-clipped and released toads outside the pool fences, but I recorded only the initial orientation of juvenile salamanders (i.e., the salamanders were not marked and released). Pitfall traps along the forest edges were checked daily for toads from 2 June to 21 August. I used HOBO H8 temperature loggers (Onset Computer Company, Bourne, Massachusetts, USA) to record air temperature at 15-min intervals at one 5-m pool (5C) and one 50-m pool (50E) from 14 June to 21 August.

Analyses

I used circular statistics to test the null hypothesis that individual movement angles at each pool were uniformly distributed (i.e., random) and, if nonrandom, whether emigrating juveniles oriented toward the nearest forest edge. I tested for nonrandom orientation using Rayleigh tests (Batschelet 1981). Although the V test is a more powerful test of uniformity when there is an expected direction (Batschelet 1981), several expected directions could be hypothesized in my study, given the variety of factors that might influence migration by juvenile amphibians. Although I was interested primarily in orientation with respect to forest, I did not want to overlook any evidence of homing toward the pond of origin or orienting toward other potential cues. The analyses were based on all first-time captures at each pool and significance tests were corrected for grouping, because each pitfall trap sampled one-eighth of the circumference of the drift fence surrounding each pool.

For pools at which movement was significantly nonrandom according to Rayleigh tests ($\alpha = 0.05$), I tested whether the movement direction deviated significantly from the direction to nearest forest based on whether the direction to the nearest forest was included in the 95% CI of the observed mean angle (μ; Batschelet 1981). I used Oriana software (Version 1.06, Kovach Computing Services, Pentraeth, Wales, UK) to graph and visually inspect the data for adherence to statistical assumptions and to calculate circular statistics, applying a grouping correction factor of 1.0262 to the mean vector length (r) provided by Oriana (Batschelet 1981). I applied these same statistical procedures to orientation data for juveniles migrating from the same pool on the same night using capture data for eight pools having $\geq$10 captures in a single night.

Because forest edges are large targets, one might not expect highly concentrated movement vectors even if individuals were exhibiting target-oriented movement. Furthermore, inability to detect the nearest forest does not imply inability to distinguish forest from nonforest. Thus, I conducted log-likelihood ratio G tests ($\alpha = 0.05$; Sokal and Rohlf 1995) on the number of salamander captures toward vs. away from forest at each pool. The number of captures toward forest was obtained by summing the captures in the two cardinal directions corresponding to the two closest forest edges.

I did not analyze orientation of emigrating toads because I could not reliably determine their initial movement direction. Although pitfall traps were highly effective for salamanders, I observed several small toads ($<$11 mm in length) climbing out of the pitfall traps and I captured many toads by hand as they hopped along the inside of the pool fences. Thus, the capture methods for toads violated the assumption that each individual would be captured by the trap on either side of its original point of contact with the fence. Because I marked and released toads outside the pool fences, however, I determined how many reached the forest from pools at different distances.

For salamanders recaptured at the forest edge, I calculated the correlation between distance to forest vs. the deviation between salamanders' initial and final bearings. If the perceptual range of juvenile salamanders is short, then salamanders leaving pools close to forest might exhibit target-oriented movement, whereas those emigrating from distant pools might not. Thus, salamanders emigrating from close pools might be expected to exhibit straighter movement paths, resulting in a smaller deviation between their initial bearing (determined by capture at the pool fence) and their final bearing (determined by capture at the forest edge fence).

I used an information-theoretic approach to evaluate several a priori models of the factors influencing migratory success of juveniles of both species. Migratory success was defined as whether a marked individual reached the forest, as determined by capture along the forest edge fences. Under this approach, a ''best'' model is identified based on the Kullback-Leibler discrepancy and the remaining models are ranked according to Akaike's Information Criterion (AIC or AIC_c to correct for small sample sizes) and Akaike weights (w); the model receiving the lowest AIC value and highest Akaike weight is the model that best approximates the data (Burnham et al. 1995). Models differing from the best model by $<$2 (i.e., $\Delta\mathrm{AIC} < 2$) are considered equally well supported and thus provide the basis for primary inference. I used simple logistic regression (PROC GENMOD, SAS Institute 1989) to model the probability that individuals did not reach forest in relation to seven predictor variables (Table 1). Capture probability (CPROB; Table 1) was calculated based on the

TABLE 1. Abbreviations and descriptions of variables included in the models of recapture at forest edge for juvenile spotted salamanders and American toads.

Variable	Description
DIST	distance (m) between pool of origin and nearest forest edge
CPROB	capture probability: percentage of area sampled by edge fences
DATE	Julian date of release
TEMP	maximum temperature (°C) on day of release
PRCP	total precipitation (inches) in 24 h following release
SIZE	body length (mm) measured at time of release
BRNG†	initial bearing: *to forest* (if straight line originating at pool center and passing through pool trap intersected the edge fence) vs. *away from forest* (if straight line originating at pool center and passing through pool trap did not intersect edge fence)

† Used only in salamander models because initial movement directions of toads could not be determined.

width of an arc bounded by imaginary lines from the pool to each end of the edge fence. Because pools located closer to forest were also more enclosed by forest, there should have been an increasing probability of recapturing marked animals as distance decreased.

I evaluated six alternative models for spotted salamanders and five for American toads (Table 2). Each set of models included a global model of all predictor variables and a null model of the intercept only. The distance model (DIST, CPROB) represents the primary hypothesis being tested. An alternative environmental model (DATE, TEMP, PRECIP, SIZE) was evaluated because of the demonstrated influence of weather conditions on amphibian migration (e.g., Shoop 1974, Kleeberger and Werner 1983, Semlitsch 1985, Sexton et al. 1990, Sinsch 1990). Hourly precipitation data were obtained from NOAA (National Climatic Data Center, Asheville, North Carolina, USA) and originated from a weather station located 5 km from the study area. Body size was included in this model because susceptibility to heat stress or desiccation could be related to size. In particular, smaller individuals would be expected to experience greater rates of evaporative water loss as a function of their greater surface area-to-volume ratio (Spight 1968). Because both distance to forest and environmental conditions could be important, I included a combination model (DIST, CPROB, TEMP, PRCP). For salamanders, I evaluated an additional model incorporating both distance variables and their initial movement direction (DIST, CPROB, BRNG, DIST*BRNG). This model included an interaction between distance to forest and initial bearing because the ability of salamanders to perceive and orient toward forest might decrease with increasing distance.

RESULTS

Fence capture rates

Capture rates at the pool and forest edge fences varied greatly between species and years, and among pools at different distances from forest (Table 3). Of the 924 salamander larvae added to pools in 2001, 473 were captured at the pool fences as emigrating juveniles. Of these, 323 were marked and released outside the pool fences, the rest having died in the traps, presumably due to heat stress. Temperatures warmed rapidly on the morning following the first major emigrations from

TABLE 2. Models of recapture at forest edge for juvenile spotted salamanders and American toads released from pools in pastures.

Model†	No. parameters	AIC_c	ΔAIC_c	*w*‡
Spotted salamander				
DIST CPROB	3	324.9	0.0	0.6787
DIST CPROB TEMP PRCP	5	327.7	2.8	0.1637
DIST CPROB BRNG DIST*BRNG	5	328.1	3.2	0.1369
DIST CPROB DATE TEMP PRCP SIZE BRNG	8	332.7	7.9	0.0134
NULL	1	334.0	9.1	0.0071
DATE TEMP PRCP SIZE	5	341.1	16.2	0.0002
American toad:				
DIST CPROB	3	197.1	0.0	0.5456
DIST CPROB DATE TEMP PRCP SIZE	7	198.2	1.1	0.3226
DIST CPROB TEMP PRCP	5	200.0	2.9	0.1298
NULL	1	208.5	11.4	0.0018
DATE TEMP PRCP SIZE	5	212.3	15.2	0.0003

† Models are ranked within each species in ascending order according to Akaike's Information Criterion (AIC_c).

‡ Akaike weight.

TABLE 3. Mean capture rates of juvenile spotted salamanders and American toads at pool fences (percentage of larvae added to pools that were recaptured as emigrating juveniles) and at edge fences (percentage of marked juveniles that were recaptured at forest edge) in 2001 and 2002.

Distance to nearest forest	Salamanders						Toads					
	2001			2002			2001			2002		
	Pools (n)	Fences		Pools (n)	Fences		Pools (n)	Fences		Pools (n)	Fences	
		Pool	Edge		Pool	Edge†		Pool	Edge‡		Pool	Edge‡
5 m	3	49.3	23.5	3	74.5		3	5.4	37.5	3	22.5	35.7
10 m	5	38.4	26.7	0			5	8.6	30.5	3	1.3	
25 m	5	58.9	22.1	3	13.8		5	7.7	7.7	3	37.5	23.1
50 m	5	57.6	9.2	0			5	1.7	0	3	35.4	9.2

† Salamanders were not marked and released outside pool fences in 2002.

‡ Average values are based on pools at which ≥4 toads were captured, marked, and released; there were <4 toad captures at all 10-m pools in 2002.

pools and before I could finish checking all the traps. The size of salamanders at the time of first capture was 28.1 ± 1.8 mm (mean ± 1 SD) from the tip of the snout to the posterior end of the vent. Of the 157 salamander larvae added to pools in 2002, 69 were captured at the pool fences.

Most of the salamander captures at pool fences (65% over both years) occurred when there had been at least trace amounts of precipitation in the preceding 24 hours. This was especially true in 2001, when 70% of captures occurred following rain events. In early summer of 2002, however, there were 14 consecutive days without precipitation and metamorphosed salamanders did not wait for rain to emigrate. Thus, only 39% of juvenile salamanders in 2002 emigrated on days with rain.

Of the 1087 toad larvae added to pools in 2001, 64 were captured, marked, and released at the pool fences. Of the 589 toad larvae added to pools in 2002, 141 were captured, marked, and released at the pool fences. In 2002, toad larvae were added to pools about one month earlier than in 2001, which may have contributed to greater larval survival in 2002. The mean size of toads (measured from the tip of the snout to the end of the urostyle) at the time of first capture was 14.8 ± 4.0 mm in 2001 and 13.5 ± 2.9 mm in 2002. Overall, 49% of the toad captures at pool fences occurred on days following rain events (39% in 2001 and 54% in 2002).

Orientation and movement behavior

Salamanders displayed directed movement at a subset of pools, but rarely was the mean direction consistent with the direction to the nearest forest edge. Orientation was significantly nonrandom at eight of 18 pools in 2001 and one of three pools in 2002 (Fig. 2). There were too few captures at the other three (25-m) pools in 2002 to permit statistical analysis (Table 3). At only one pool out of nine was the mean angle consistent with target-oriented movement toward the nearest forest (25E; Fig. 2). At all others, the bearing to the nearest forest fell outside the 95% CI of the mean angle. Juvenile salamanders tended to orient nonrandomly at five of the eight pools having at least 10 captures on a night of heavy migration (either 15 June or 2 July 2001), according to Rayleigh tests corrected for grouping: 25B ($r_c = 0.44$, $P = 0.028$, $n = 18$), 25E ($r_c = 0.33$, $P = 0.065$, $n = 25$), 50A ($r_c = 0.37$, $P = 0.048$, $n = 22$), 50B ($r_c = 0.43$, $P = 0.074$, $n = 14$), and 50C ($r_c = 0.64$, $P < 0.001$, $n = 17$). At only one of these five pools (25E) was the mean angle consistent with direction toward the nearest forest.

Qualitatively similar results were obtained by analyzing captures classified as toward vs. away from forest. Although the majority of emigrating salamanders at most pools oriented in the general direction of forest, the null hypothesis of equal number of captures was rejected at only five of 18 pools in 2001 and one of three pools in 2002 (Table 4). Furthermore, the difference at pool 10D was in the direction opposite that predicted.

The distance of pools from forest did not significantly influence movement patterns of emigrating salamanders. Salamanders oriented nonrandomly at an equal number of pools within each distance category (Fig. 2). Distance to forest and magnitude of the deviation between initial and final bearings were not correlated ($r_S = 0.09$, $n = 33$, $P = 0.6126$). At the more distant pools, however, there was a greater tendency for marked salamanders to return to the pools, resulting in recaptures of some individuals back inside the pool fences. There were seven such ''reversals'' at 50-m pools, six at 25-m pools, three at 10-m pools, and one at 5-m pools, corresponding to 8.0%, 5.8%, 3.8%, and 1.9%, respectively, of the total number of salamanders marked at each distance.

Migratory success

Of the 323 salamanders marked and released outside pool fences in 2001, 76 were later recaptured along the forest edge. Of the 205 toads marked and released outside pool fences over both years of the study, 46 were recaptured along the forest edge. Some juveniles managed to bypass the pool fences, as evidenced by the

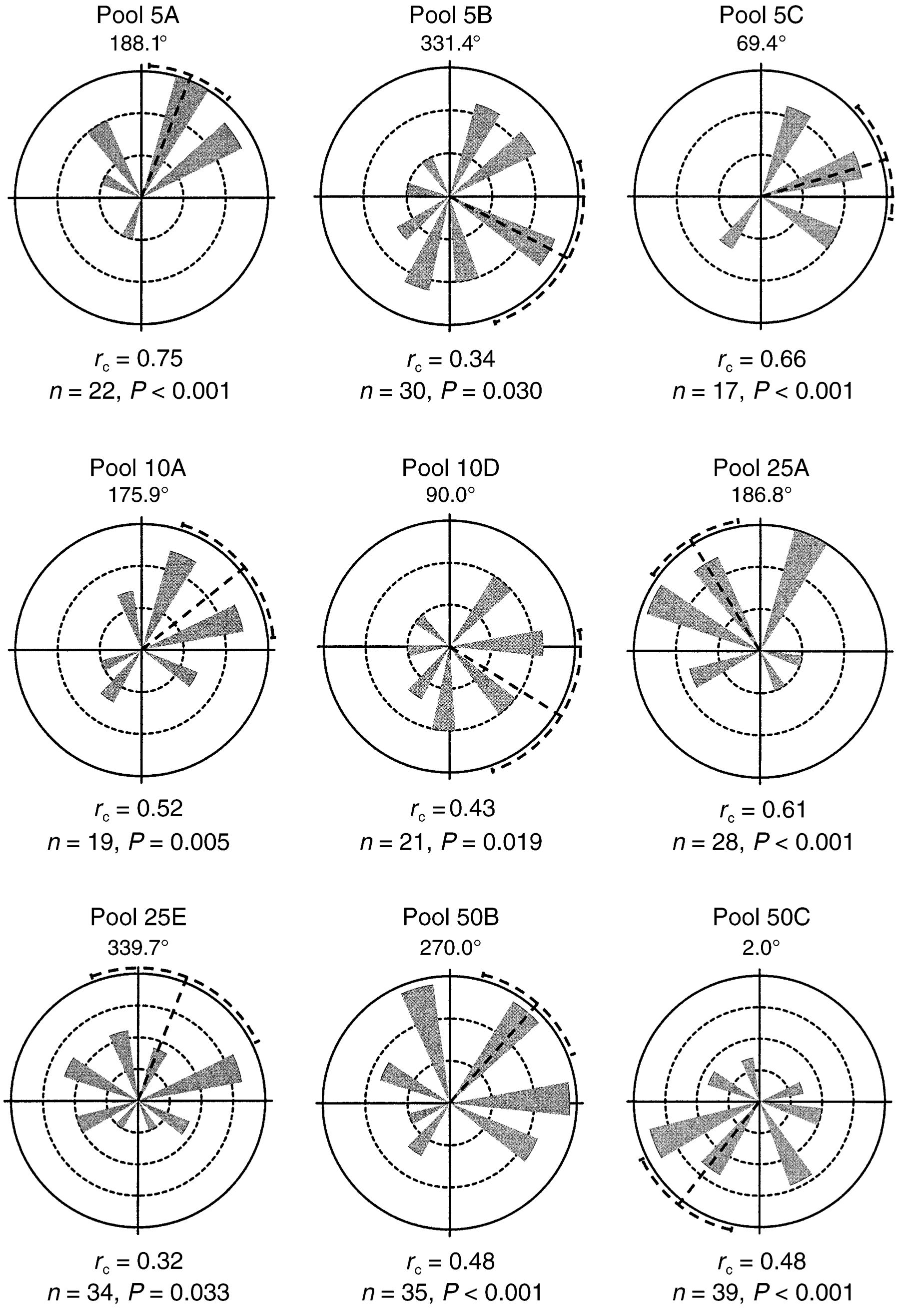

FIG. 2. Circular histograms (rose diagrams) of capture frequencies of salamanders at eight pools with nonrandom orientation in 2001 and one pool (5A) with nonrandom orientation in 2002. Dotted lines are the mean angles (μ) with 95% confidence intervals, and mean vector lengths (r_c) are corrected for grouping. For ease of interpretation, the angular data were transposed so the direction to the nearest forest edge is at the top of each graph.

capture of 66 unmarked salamanders at the edge fences. These animals could not be included in the analyses because their pools of origin were unknown. For both salamanders and toads, the percentage of marked animals recaptured at the forest edge declined greatly with increasing distance between the pools and the nearest forest (Table 3).

A simple recapture model that included DIST and CPROB proved to be the best model for both species, although for toads the global model with all five variables was also well supported (ΔAIC = 1.1; Table 2). The best model for salamanders was more than four times better supported than the next best model, which included parameters reflecting environmental conditions

TABLE 4. Number of salamander captures toward and away from forest at each pool.

Pool	Number of captures: Toward	Number of captures: Away	G†
5 m from forest			
5A (2001)	15	12	0.3340
(2002)	20	2	**17.0945**
5B (2001)	18	12	1.2081
(2002)	8	6	0.2867
5C (2001)	15	2	**11.2518**
(2002)	14	8	1.6573
10 m from forest			
10A	16	3	**9.7654**
10B	15	8	2.1646
10C	10	6	1.0107
10D	6	15	**3.9849**
10E	9	10	0.0527
25 m from forest			
25A	16	12	0.5734
25B	18	17	0.0286
25C	18	13	0.8100
25D	9	10	0.0527
25E	22	12	2.9851
50 m from forest			
50A	16	23	1.2632
50B	27	8	**10.8922**
50C	18	21	0.2310
50D	20	8	**5.3131**
50E	8	5	0.6986

† Log-likelihood ratio test statistic; bold values exceeded critical value of 3.84 ($\alpha = 0.05$, df = 1).

at the time of release. Models lacking distance parameters ranked the lowest for both species (Table 2).

Odds ratios were calculated directly from the estimated regression coefficients (Allison 1991) for all parameters in the best supported models; parameter estimates are presented for both the best and second-best models for toads to reflect model selection uncertainty (Table 5). The odds ratios have a straightforward interpretation (Allison 1991). For salamanders, every 1-m increase in distance between a pool and the nearest forest resulted in an estimated 4.5% decrease in probability of recapture at the forest edge. The 95% confidence limits for odds of capture probability included 1.0, suggesting that this parameter had little effect on recapture rate. Thus, although DIST and CPROB were negatively correlated (for salamanders, Pearson $r = -0.903$, $P < 0.001$; for toads, $r = -0.927$, $P < 0.001$), the parameter estimates indicate that DIST, rather than CPROB, was the most important variable influencing recapture rate. The same holds true for toads, with recapture probability estimated to decrease by ~7% for every 1-m increase in distance (Table 5). To enhance the generality of my results to other landscapes in which the spatial arrangement of ponds and forests is likely to differ from my study area, I used the best model for each species (Table 5) to generate predicted probabilities of reaching forest, while holding CPROB constant at the mean value (Fig. 3). CPROB varied across pools from 49.8% to 84.1%, with a mean value of 72.6% for salamanders and 71.5% for toads. Although the parameter estimates shown in Table 5 were derived by modeling the probability of not reaching forest (yielding a more intuitive interpretation of the odds ratios), the predicted relationship in Fig. 3 was derived by modeling the probability of reaching forest.

The recapture probability of toads decreased slightly for individuals released later in the season (an estimated 2.5% decrease for each day). Body size did not appear to influence migratory success for either species (Tables 2 and 5). Likewise, neither TEMP nor PRCP were important variables in models of recapture probability (Tables 2 and 5).

DISCUSSION

Juvenile salamanders in this study generally failed to exhibit target-oriented behavior during their initial emigration into the terrestrial environment. I presumed that newly metamorphosed spotted salamanders would orient toward the nearest forest if they could detect it, because it would be advantageous to minimize the amount of time spent in the pasture. Rothermel and Semlitsch (2002) found that juvenile ambystomatid salamanders and American toads emigrating from pools on forest edges showed a significant preference for forest and experienced significantly lower rates of dehydration in forests than in fields during 24-hour dehydration trials. Although Malmgren (2002) noted that amphibians may begin to orient with respect to the surrounding terrestrial habitat while still in the larval phase, the lack of oriented movement observed in my study cannot be attributed simply to larvae having insufficient time in the pools to detect necessary cues. Rothermel and Semlitsch (2002) also head-started larvae in cattle tanks before transferring them to pools, suggesting that exposure to terrestrial cues throughout

TABLE 5. Parameter estimates, odds ratios, and confidence limits for parameters in the best recapture model for juvenile spotted salamanders and the best and second-best recapture models for juvenile American toads.

Parameter	Parameter estimate (β)	Odds ratio	95% confidence limits
Spotted salamander			
DIST	0.0438	1.045	1.005, 1.086
CPROB	0.0250	1.025	0.957, 1.099
American toad			
Model 1			
DIST	0.0694	1.072	1.019, 1.128
CPROB	0.0510	1.052	0.965, 1.147
Model 2			
DIST	0.0667	1.069	1.015, 1.126
CPROB	0.0303	1.031	0.942, 1.128
DATE	0.0248	1.025	1.002, 1.049
TEMP	−0.0057	0.994	0.884, 1.119
PRCP	−0.1744	0.840	0.441, 1.600
SIZE	−0.0931	0.911	0.806, 1.030

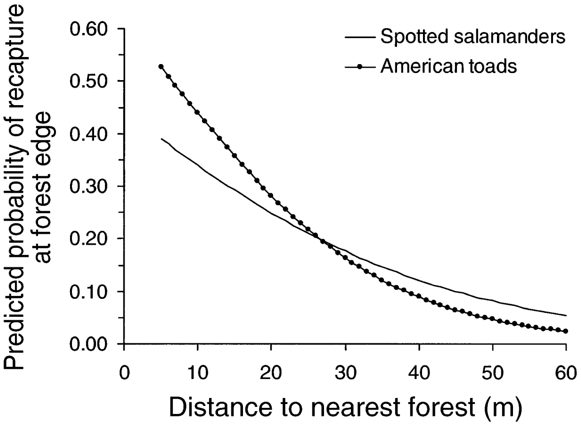

FIG. 3. Relationship between probability of reaching forest and distance to nearest forest for juvenile spotted salamanders and American toads. Predicted probabilities were generated using the parameter estimates and best recapture models for each species shown in Table 5 and holding capture probability constant at the mean value. For salamanders, $P(\text{recap}) = 1/(1 + \exp[-1.586 + 0.0438(\text{DIST}) + 0.0250(72.61)])$; for toads, $P(\text{recap}) = 1/(1 + \exp[-4.0978 + 0.0694(\text{DIST}) + 0.0510(71.53)])$.

the entire larval period is not essential for postmetamorphic orientation. It remains unknown whether amphibians perceive and begin responding to terrestrial cues as larvae or whether the perception of such cues is restricted to the period just preceding or during postmetamorphic emigration.

There are several alternative explanations for the observed lack of target-oriented movement. Juvenile spotted salamanders may indeed have such a limited perceptual range that they cannot detect forest from even a few meters. As Lima and Zollner (1996) noted, habitat fragmentation is a relatively recent occurrence from an evolutionary standpoint; therefore, forest-associated salamanders simply may not have evolved long-distance perceptual abilities even in the presence of recent, strong selection. Alternatively, if the distances between pools and forest in my experiment (<50 m) could be traversed easily by emigrating juveniles, then perhaps they were not motivated to take the most efficient movement path. This seems unlikely, however, considering the low recapture rates of juveniles from even relatively close pools (Table 3). Another possibility is that reliable cues indicating direction to forest could be lacking. The visual range of salamanders is almost certainly limited by ground-level vegetation and the dark, rainy conditions under which migration typically occurs (Shoop 1965, Semlitsch 1985). Over short distances, olfactory cues could be more useful, but shifting winds might make them an unreliable source of long-range directional information. Sjogren-Gulve (1998) implicated olfaction or attraction to breeding choruses in the apparent target-oriented movement of juvenile pool frogs toward neighboring ponds ≥ 270 m away, but these patterns could more easily be explained by the presence of suitable nonbreeding habitat (marshes) between the ponds. Neither vegetation differences nor conspecific acoustic cues could account for the migratory patterns of juvenile amphibians in my study.

Previous studies of natural ponds have documented nonrandom patterns of emigration by cohorts of recently metamorphosed amphibians (e.g., Semlitsch 1985, Stenhouse 1985, Windmiller 1996, Dodd and Cade 1998, Malmgren 2002), but the underlying basis for these patterns remains largely unknown. I observed directed movements at a subset of pools, suggesting that emigrating salamanders at those pools perceived and responded similarly to some kind of cue. If salamanders were homing to the pond where eggs were collected (which seems unlikely, considering the distances involved), then there should have been a common, southward orientation; instead, mean directions varied greatly among pools. Likewise, a response to a windborne cue might have generated a common direction independent of the direction to the nearest forest for a given pool. Again, though, the directions varied. One intriguing, but not well-supported, idea is that chemically mediated social interactions may influence movements, such that juveniles might follow scent trails left by adults or other juveniles (Hayward et al. 2000, Malmgren 2002). Because I observed biased orientation of salamanders emigrating on the same night at some pools, I cannot rule out the possibility that positive interactions, such as trailing behavior, influenced migratory directions. On the other hand, trailing an equally naïve juvenile into the terrestrial environment hardly seems like an effective strategy.

There were no obvious physical differences between the pools at which salamanders exhibited nonrandom vs. random orientation. Although the pastures tended to slope gently toward the forest edges, all pools had similar slopes ($<6\%$). Because emigration direction varied even among the pools having nonrandom orientation, differences in microtopographic features within the area enclosed by each pool fence may have funneled emigrating salamanders in a particular direction. Thus, juveniles leaving ponds for the first time probably responded similarly to physical cues in the immediate terrestrial environment, such as moisture gradients or topographic features, rather than to distant cues.

The higher number of reversals by salamanders at more distant pools suggests that salamanders that fail to locate suitable habitat during their initial emigration sometimes return to their natal pond, which is the only known landmark for juveniles migrating for the first time. In a study of spotted salamanders at a pond on a forest–grassland edge, juveniles that emigrated toward the grassland reversed direction significantly more often than those that initially emigrated toward the forest (Rittenhouse 2002). Rothermel and Semlitsch (2002) also observed this behavior in juvenile spotted and small-mouthed salamanders emigrating from artificial pools on forest–field edges; six of 16 juvenile salamanders that initially migrated into fields returned to their pools, whereas none of the 36 salamanders that migrated into the forest returned to the pools.

Despite differences in behavior, both species demonstrated similar migratory ability in my study. The juvenile amphibians not recaptured after they left the pools either dispersed outside the fenced area or died in the fields. The low number of recaptures at the forest edges may have resulted from mortality due to heat stress. Mean daily maximum temperatures in the pastures in July of 2002 averaged 41.9°C, exceeding the critical thermal maximum for juvenile spotted salamanders (39.7°C; Pough and Wilson 1970). Ambystomatid salamanders migrate only at night and their movements are highly correlated with rainfall. In Shoop's (1974) study, four metamorphosed spotted salamanders that sought shelter in mud and debris at the edge of a pond desiccated and died while waiting for a rainy night to emigrate. In the second year of my study, a large number of postmetamorphic salamanders emigrated from the pools during a prolonged dry period, chancing emigration rather than waiting for more suitable conditions. Such behavior could be more common at pools in open habitats, where temperatures are much higher and terrestrial refuges (e.g., leaf litter) may be scarce. Unlike salamanders, postmetamorphic toads are active diurnally (Tracy 1971; *personal observation*). Their movements also appear to be less constrained by rainfall; half of the toads in my study emigrated from pools on days without rain.

Although environmental conditions have been shown to be important factors influencing the timing of migration and movement patterns of adult and juvenile amphibians, the migratory success of individuals in this study did not depend on environmental conditions immediately following their release. Of the salamander captures, 70% occurred within 24 hours of rain events. Thus, soil moisture in the pastures tended to be uniformly high at the time of releases, making subsequent precipitation less important. The lack of a relationship between environmental conditions and migratory success also may have been an artifact of the capture method. Because individuals were intercepted at the pool fences and then released the following morning, environmental conditions were somewhat uncoupled from the actual emigration event. In general, the percentage of juveniles reaching the forest was probably underestimated in this study, because initial migratory movements were interrupted and because drift fences do not attain 100% capture efficiency. This bias, however, is independent of distance from forest.

Implications for amphibian conservation

The results of my study have important implications for maintaining connectivity between aquatic and terrestrial habitats, specifically for determining how landscape complementation may constrain amphibian population persistence in highly fragmented landscapes. Understanding movement behavior and dispersal ability of juveniles is especially important because, in many species, juveniles are responsible for most interpond dispersal (Gill 1978, Berven and Grudzien 1990, Sjogren-Gulve 1994). They may also respond differently to habitat alteration than do adults, which are familiar with the landscape and experience lower rates of evaporative water loss because of their larger size (Spight 1968). The population-level consequence of random juvenile emigration is that, at breeding sites in pastures or other open habitats, a large percentage of each year's juvenile cohort is likely to perish in unsuitable habitat. The same occurs if migratory movements are biased by features of the pond itself, because such features may bear no relation to the location of suitable terrestrial habitat. Thus, ponds surrounded by pastures or croplands might be population sinks because of decreased juvenile survival during emigration. In situations like this, evidence of breeding activity and even of juvenile production (i.e., successful metamorphosis) might be unreliable indicators of habitat quality.

There are essentially two options for ensuring landscape complementation for pond-breeding amphibians. The first is to use information on migratory behavior and success to determine acceptable distances between aquatic and terrestrial habitats, given inevitably high losses to the matrix. Under this approach, the goal is to identify what level of additional juvenile mortality local populations can sustain without becoming sinks, and at what distance that level is exceeded. Conservation efforts could then focus on protecting or restoring wetlands that meet this threshold distance, as such sites are likely to enhance persistence at a metapopulation or regional scale. Intensive population studies of pond-breeding amphibians have revealed that local extinction is a fairly common event (Semlitsch et al. 1996, Marsh and Trenham 2001) and that the status of a given breeding site as a source or sink population may change over time (Gill 1978).

A population model developed for *Ambystoma opacum* implied that, in the absence of immigration, postmetamorphic survival had to exceed 70% to maintain the local population (Taylor and Scott 1997). Likewise, Trenham et al. (2000) found that survival to first reproduction had to exceed 18% to sustain the population of *A. californiense* that they studied. In my study, an average of only 9% (range 0–14%) of juvenile *A. maculatum* released from 50-m pools apparently survived their initial migration into the terrestrial environment. If the estimates of Taylor and Scott (1997) and Trenham et al. (2000) are representative of ambystomatid population dynamics, then my results suggest that the threshold distance needed to ensure adequate survival of postmetamorphic ambystomatids is <50 m.

This threshold distance might have to be adjusted downward for cases in which the surrounding land use is extremely hostile (e.g., row-crop agriculture, residential) or in which there is very little terrestrial habitat remaining in the landscape. In situations of more extreme forest fragmentation, ''target'' forest patches probably would be smaller, with a corresponding reduction in interception probability dependent on distance and the shape or orientation of the forest patch relative to the breeding site (Bowman et al. 2002). The landscape used for my study retains ~40% forest cover (*unpublished data*) and the pastures were nearly enclosed by forest; thus juveniles had a high probability of intercepting forest (represented by the variable, CPROB; Table 1). The predicted relationship between migratory success and distance shown in Fig. 3, however, is independent of capture probability and thus can be interpreted as the landscape resistance (Ricketts 2001) encountered by migrating juvenile amphibians in the pastures used in my study.

A second approach would attempt to minimize losses to the matrix by maintaining direct habitat connectivity (i.e., corridors) between aquatic and terrestrial habitats. Movement corridors might not have to consist of mature, closed-canopy forest, as long as they provide adequate cover and microclimatic conditions conducive to survival of the target species and life stage. With effective corridors, breeding sites and terrestrial habitats potentially could be separated by longer distances while still maintaining sustainable migratory rates. The effectiveness of corridors depends greatly on species- and life-stage-specific behaviors (Haddad 1999, Rothermel and Semlitsch 2002). Some amphibian species do not avoid agricultural or other heavily disturbed areas (e.g., California red-legged frogs; Bulger et al. 2003); thus, species-specific information on habitat use during migration is needed. In general, those species exhibiting the greatest behavioral avoidance of the matrix would be the most likely to preferentially use the corridor, thus minimizing losses to the matrix. Clearly, additional research is needed to test the effectiveness of either of these management approaches before implementing them at a broad scale. Finally, as observed for other phenomena (e.g., edge effects; Donovan et al. 1997), landscape context must be considered because a high degree of fragmentation may need to be reached before landscape complementation becomes a significant constraint on amphibian population persistence.

ACKNOWLEDGMENTS

I am indebted to A. Nold, Z. Slinker, J. Deters, S. Rothermel, C. R. Mank, L. Murray, M. Doyle, T. Green Rittenhouse, S. James, and A. Gellatly for their assistance in the field and dedication to the pursuit of science, albeit cleverly disguised as trench-digging, backfilling, trap-checking, and truck-pushing. Ray Semlitsch and Frank Thompson provided invaluable support and advice, and two anonymous reviewers offered helpful suggestions for improving the manuscript. This study was funded by the North Central Research Station of the U.S. Forest Service and the Division of Biological Sciences at the University of Missouri. Manuscript preparation was supported in part by the Environmental Remediation Sciences Division of the Office of Biological and Environmental Research, U.S. Department of Energy through Financial Assistance Award Number DE-FC09-96SR18546 to the University of Georgia's Research Foundation.

LITERATURE CITED

Allison, P. D. 1991. Logistic regression using the SAS System. SAS Institute, Cary, North Carolina, USA.

Batschelet, E. 1981. Circular statistics in biology. Academic Press, London, UK.

Berven, K. A., and T. A. Grudzien. 1990. Dispersal in the wood frog (*Rana sylvatica*): implications for genetic population structure. Evolution **44**:2047–2056.

Bowman, J., N. Cappuccino, and L. Fahrig. 2002. Patch size and population density: the effect of immigration behavior. Conservation Ecology **6**(1):9. ⟨http://www.consecol.org/vol6/iss1/art9⟩

Bulger, J. B., N. J. Scott, Jr., and R. B. Seymour. 2003. Terrestrial activity and conservation of adult California red-legged frogs *Rana aurora draytonii* in coastal forests and grasslands. Biological Conservation **110**:85–95.

Burnham, K. P., G. C. White, and D. R. Anderson. 1995. Model selection strategy in the analysis of capture–recapture data. Biometrics **51**:888–898.

deMaynadier, P. G., and M. L. Hunter, Jr. 1999. Forest canopy closure and juvenile emigration by pool-breeding amphibians in Maine. Journal of Wildlife Management **63**:441–450.

Dodd, C. K., Jr., and B. S. Cade. 1998. Movement patterns and the conservation of amphibians breeding in small, temporary wetlands. Conservation Biology **12**:331–339.

Donavan, L. A. 1980. Morphological features of the stages in the development of *Ambystoma talpoideum* (Holbrook) from the fertilized egg to the adult. Dissertation. University of Southern Mississippi, Hattiesburg, Mississippi, USA.

Donovan, T. M., P. W. Jones, E. M. Annand, and F. R. Thompson, III. 1997. Variation in local-scale edge effects: mechanisms and landscape context. Ecology **78**:2064–2075.

Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos **65**:169–175.

Gibbs, J. P. 1998. Amphibian movements in response to forest edges, roads, and streambeds in southern New England. Journal of Wildlife Management **62**:584–589.

Gill, D. E. 1978. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). Ecological Monographs **48**:145–166.

Gosner, K. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica **16**:183–190.

Haddad, N. M. 1999. Corridor use predicted from behaviors at habitat boundaries. American Naturalist **153**:215–227.

Hayward, R., R. S. Oldham, P. J. Watt, and S. M. Head. 2000. Dispersion patterns of young great crested newts (*Triturus cristatus*). Herpetological Journal **10**:129–136.

Joly, P., and C. Miaud. 1993. How does a newt find its pond? The role of chemical cues in migrating newts (*Triturus alpestris*). Ethology Ecology and Evolution **5**:447–455.

Joly, P., C. Miaud, A. Lehmann, and O. Grolet. 2001. Habitat matrix effects on pond occupancy in newts. Conservation Biology **15**:239–248.

Kleeberger, S. R., and J. K. Werner. 1983. Post-breeding migration and summer movement of *Ambystoma maculatum*. Journal of Herpetology **17**:176–177.

Lima, S. L., and P. A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology and Evolution **11**:131–135.

Malmgren, J. C. 2002. How does a newt find its way from a pond? Migration patterns after breeding and metamorphosis in great crested newts (*Triturus cristatus*) and smooth newts (*T. vulgaris*). Herpetological Journal **12**:29–35.

Marsh, D. M., and P. C. Trenham. 2001. Metapopulation dynamics and amphibian conservation. Conservation Biology **15**:40–49.

McGregor, J. H., and W. R. Teska. 1989. Olfaction as an orientation mechanism in migrating *Ambystoma maculatum*. Copeia 1989:779–781.

Oldham, R. S. 1966. Spring movements in the American toad, *Bufo americanus*. Canadian Journal of Zoology **44**:63–100.

Pope, S. E., L. Fahrig, and H. G. Merriam. 2000. Landscape complementation and metapopulation effects on leopard frog populations. Ecology **81**:2498–2508.

Pough, F. H., and R. E. Wilson. 1970. Natural daily temperature stress, dehydration, and acclimation in juvenile *Ambystoma maculatum* (Shaw) (Amphibia: Caudata). Physiological Zoology **43**:194–205.

Ricketts, T. H. 2001. The matrix matters: effective isolation in fragmented landscapes. American Naturalist **158**:87–99.

Rittenhouse, T. A. G. 2002. Spotted salamander migration at a pond located on a forest–grassland edge. Thesis. University of Missouri, Columbia, Missouri, USA.

Rothermel, B. B., and R. D. Semlitsch. 2002. An experimental investigation of landscape resistance of forest versus old-field habitats to emigrating juvenile amphibians. Conservation Biology **16**:1324–1332.

SAS Institute. 1989. SAS user's guide. Version 6. SAS Institute, Cary, North Carolina, USA.

Semlitsch, R. D. 1981. Terrestrial activity and summer home range of the mole salamander (*Ambystoma talpoideum*). Canadian Journal of Zoology **59**:315–322.

Semlitsch, R. D. 1985. Analysis of climatic factors influencing migrations of the salamander *Ambystoma talpoideum*. Oecologia **65**:305–313.

Semlitsch, R. D. 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. Conservation Biology **12**:1113–1119.

Semlitsch, R. D. 2000. Principles for management of aquatic-breeding amphibians. Journal of Wildlife Management **64**: 615–631.

Semlitsch, R. D., and J. R. Bodie. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology **17**:1219–1228.

Semlitsch, R. D., D. E. Scott, J. H. K. Pechmann, and J. W. Gibbons. 1996. Structure and dynamics of an amphibian community: evidence from a 16-year study of a natural pond. Pages 217–248 *in* M. L. Cody and J. A. Smallwood, editors. Long-term studies of vertebrate communities. Academic Press, San Diego, California, USA.

Sexton, O. J., C. Phillips, and J. E. Bramble. 1990. The effects of temperature and precipitation on the breeding migration of the spotted salamander (*Ambystoma maculatum*). Copeia 1990:781–787.

Shoop, C. R. 1965. Orientation of *Ambystoma maculatum*: movements to and from breeding ponds. Science **149**:558–559.

Shoop, C. R. 1974. Yearly variation in larval survival of *Ambystoma maculatum*. Ecology **55**:440–444.

Sinsch, U. 1990. Migration and orientation in anuran amphibians. Ethology Ecology and Evolution **2**:65–79.

Sjogren-Gulve, P. 1994. Distribution and extinction patterns within a northern metapopulation of the pool frog, *Rana lessonae*. Ecology **75**:1357–1367.

Sjogren-Gulve, P. 1998. Spatial movement patterns in frogs: target-oriented dispersal in the pool frog, *Rana lessonae*. Ecoscience **5**:31–38.

Skelly, D. K., E. E. Werner, and S. A. Cortwright. 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. Ecology **80**:2326–2337.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. Third edition. W. H. Freeman, New York, New York, USA.

Spight, T. M. 1968. The water economy of salamanders: evaporative water loss. Physiological Zoology **41**:195–203.

Stenhouse, S. L. 1985. Migratory orientation and homing in *Ambystoma maculatum* and *Ambystoma opacum*. Copeia 1985:633–637.

Taylor, B., and D. E. Scott. 1997. Effects of larval density dependence on population dynamics of *Ambystoma opacum*. Herpetologica **53**:132–145.

Tracy, C. R. 1971. Evidence for the use of celestial cues by dispersing immature California toads (*Bufo boreas*). Copeia 1971:145–147.

Trenham, P. C., H. B. Shaffer, W. D. Koenig, and M. R. Stromberg. 2000. Life history and demographic variation in the California tiger salamander. Copeia 2000:365–377.

Whitford, W. G., and A. Vinegar. 1966. Homing, survivorship, and overwintering of larvae in spotted salamanders, *Ambystoma maculatum*. Copeia 1966:515–519.

Windmiller, B. S. 1996. The pond, the forest, and the city: spotted salamander ecology and conservation in a human-dominated landscape. Dissertation. Tufts University, Medford, Massachusetts, USA.

Zollner, P. A. 2000. Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes. Landscape Ecology **15**:523–533.