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Terrestrial distribution of pond-breeding salamanders around an isolated wetland

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Abstract. Terrestrial habitats surrounding isolated wetlands are a critical resource for many pond-breeding amphibian species, yet few studies have examined the terrestrial distribution of post-metamorphic juveniles and adults. We used an encircling drift fence at a breeding pond in conjunction with partial fences at 90, 172, and 332 m from the wetland to estimate the terrestrial distribution of adult marbled salamanders (*Ambystoma opacum*; four breeding seasons) and mole salamanders (*A. talpoideum*; two seasons), as well as the dispersion of newly metamorphosed *A. opacum* (one summer). For newly metamorphosed *A. opacum*, 79% emigrated <90 m from the wetland, and 8% moved beyond 172 m; movement distance was unrelated to body size. Distribution of adult *A. opacum* varied among years, with an average of 28% (range 23–31%) occurring beyond 172 m in all years. Averaged across two years, 51% of adult *A. talpoideum* occurred beyond 172 m. Lognormal models provided a good fit to both the juvenile and adult ambystomatid distributions, and parameters differed between age classes, sexes, species, and years within species. For adult *A. opacum* a buffer radius of 300 m or 340 m, depending on the year, is estimated to include 95% of adults; for *A. talpoideum* the estimate is 464 m or 501 m. A reanalysis of distribution data for seven ambystomatid species shows that a previous estimate of a 164-m radius to protect 95% of a population underestimates the needed buffer radius by 185 m. Because our study wetland requires a nearly 500 m wide radius to protect 95% of its ambystomatid adults, preservation of similar communities may require much more surrounding terrestrial habitat than previously thought.

Key words: Ambystoma opacum; Ambystoma talpoideum; *dispersal; isolated wetland; juvenile emigration; pond-breeding salamander; terrestrial buffer zone; terrestrial distribution.*

INTRODUCTION

Biodiversity is declining worldwide, as has been noted for numerous taxa including amphibians (Houlahan et al. 2000, Stuart et al. 2004). Of the six leading hypotheses for causes underlying population declines, most researchers agree that habitat loss and modification is of great significance (Wilcove et al. 1998). For pond-breeding amphibians with complex life cycles, habitat loss, alteration, degradation, and fragmentation may occur at both wetland breeding sites and surrounding terrestrial habitats (Gibbs 2000, Marsh and Trenham 2001).

Studies of the relationship between landscape characteristics and amphibian distribution patterns generally find negative associations between amphibian abundance and terrestrial habitat disturbance (Hecnar and M'Closkey 1996, Knutson et al. 1999); in forested ecosystems, the areal extent of forest adjacent to the wetland breeding site is of particular importance (Gibbs 1998, Guerry and Hunter 2002). In nonforested ecoregions, such as prairie or grassland/shrub habitats, the landscape surrounding wetlands also affects regional species richness (Lehtinen et al. 1999) and population size (e.g., the California tiger salamander, *Ambystoma californiense* [Trenham and Shaffer 2005]). Critical thresholds of the extent of upland undisturbed habitat needed for population persistence may vary among species due to differences in their terrestrial habitat needs and preferences (Homan et al. 2004, Cushman 2006).

At the landscape level, many amphibian species are thought to form metapopulations that rely on terrestrial connectivity among wetlands (Marsh and Trenham 2001). But no matter whether viewed at the metapopulation (landscape) or the local population (single breeding pond) scale, terrestrial habitats adjacent to wetland breeding sites are extremely important to population dynamics through effects on post-metamorphic processes such as terrestrial survival and immigration (Taylor and Scott 1997). A core terrestrial habitat surrounding wetland breeding sites is essential to maintain local populations of amphibians (Semlitsch and Bodie 2003), as it facilitates landscape-level

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processes (e.g., inter-pond dispersal and recolonization through connections to other core areas) while providing individual-level resource needs (e.g., feeding opportunities, refugia).

Despite general agreement on the need for a core terrestrial habitat for pond-breeding amphibians, few studies have examined the terrestrial distribution of metamorphs and adults around natal ponds due to relatively low recapture rates of animals with increasing distance from the pond. Determination of the core terrestrial habitat required for maintaining populations hinges on knowledge of the distance and distribution of animals as they migrate to the uplands. For pond-breeding ambystomatid salamanders a terrestrial "life zone" of 164 m around breeding sites has been proposed (plus 50-m buffer = 214-m "core habitat"), based on data from adults of six species and juveniles of two (Semlitsch 1998). Because local population dynamics in amphibians are extremely sensitive to terrestrial survival of juveniles and adults (Taylor and Scott 1997, Hels and Nachman 2002, Trenham and Shaffer 2005, Taylor et al. 2006), a crucial first step in predicting how the loss of habitat will cause population declines is understanding the terrestrial distribution of all life stages in unaltered habitat.

In this study, we used concentric rings of partial drift fence-pitfall trap arrays at 90, 172, and 332 m from a breeding pond to determine the distribution of a marked cohort of >10 000 emigrating newly metamorphosed marbled salamanders, *Ambystoma opacum*; larval density manipulations were used to generate a size disparity in a subset of metamorphs to examine potential body size effects on migration distance. The same capture arrays were used to determine the terrestrial adult distribution of *A. opacum* (in four breeding seasons) and the mole salamander (*A. talpoideum*, two seasons) during breeding immigrations to the wetland. We used these data to examine species, life-stage, sex, and year effects on migration distances and terrestrial habitat distribution patterns. We also combined our results with other studies to reassess the validity of the 164-m benchmark proposed to protect ambystomatid populations around isolated wetlands.

MATERIALS AND METHODS

Study organisms

The marbled salamander occurs across much of the eastern United States, and the mole salamander occurs on the Coastal Plain from South Carolina to eastern Texas, and north along the Mississippi River Valley to southern Illinois (Petranka 1998). In late summer or autumn, adult *A. opacum* migrate to breed in ponds that are partially or completely dry. Terrestrial adult *A. talpoideum* generally migrate to wetlands from late fall through winter and breed aquatically (Petranka 1998). After metamorphosis, juvenile salamanders migrate from the pond margin to terrestrial habitats, where they may remain from one to six years before returning to breed for the first time (Scott 1994, Pechmann 1995). Terrestrial juveniles and adults occur in forested uplands, including hardwood, pine, and mixed pine–hardwood forests (Scott 2005).

Study site

We studied the terrestrial distribution of ambystomatid salamanders at Ginger's Bay (GB), a 1.2-ha seasonal wetland on the United States Department of Energy's Savannah River Site in Aiken County, South Carolina, USA. GB is surrounded by a 15.6-ha tract that comprises a partial 200-m buffer around the wetland (Appendix A: Fig. A1). The upland is pine, pine–hardwood, and mesic hardwood communities with red maple (*Acer rubrum*), oaks (*Quercus* spp.), and loblolly pine (*Pinus taeda*). The closest known alternative amphibian breeding sites to GB are Okie Bay (375 m south of GB), and a small floodplain wetland (740 m southeast).

We used a complete encircling drift fence around the GB breeding site (Scott 1990) to capture newly metamorphosed *A. opacum* and immigrating adults of *A. opacum* and *A. talpoideum*. Based on prior long-term studies of breeding phenology (Semlitsch et al. 1996), we defined the reproductive season for *A. opacum* as September–December, and October–March for *A. talpoideum*; during these reproductive windows, the gonads of males are obviously swollen and gravid females are discernibly fattened. We defined the amphibian reproductive year to match the wetland hydrologic cycle of filling and drying; e.g., *A. opacum* breeding in the fall of 2001 were assigned to the year 2002. Adult migrations were studied in 2002, 2003, 2006, and 2007. Juvenile emigration of *A. opacum* was characterized in 2005. Drift fence buckets (19 L, $n = 28$ pairs) at the wetland were checked each morning, and one or two times per night during large migrations. In May 2005 we used minnow traps to capture metamorphs along a flooded 50-m section of the fence.

One goal of our study was to investigate the relationship between body size at metamorphosis and migration distance of juveniles. To create a suitable size disparity we manipulated larval density (4 or 12 larvae/m^2) in six aquatic enclosures in GB (see Scott 1990). At metamorphosis, individuals were collected from the wetland and the enclosures, measured, assigned to one of two size classes (<41 mm SVL or ≥41 mm), and cohort marked according to size. Metamorphs were toe-clipped for cohort identification by clipping two adjacent toes on one front foot (Ott and Scott 1999), and subsets of animals were weighed to the nearest 0.01 g and measured (snout–vent length, SVL) to within 0.5 mm; animals to be weighed were held for one day on moist paper towels in an effort to ensure comparable hydration. When captures of >2500 individuals precluded immediate processing, animals were held at 6°C in a walk-in cooler, processed in order of capture, and

TABLE 1. Capture totals and terrestrial distribution estimates for newly metamorphosed (<6 months old) *Ambystoma opacum* at three distances around the Ginger's Bay (Aiken County, South Carolina, USA) wetland in April–September 2005.

Terrestrial zone	Circumference at outer distance	Proportion fenced	Total captures	Percent distribution
Inner (0 m)	402 m	1.00	10 395 (10 118/277)	—
Zone 1 (>0–90 m)	968 m	0.116	231 (227/4)	78.8
Zone 2 (>90–172 m)	1483 m	0.151	155 (154/1)	13.5
Zone 3 (>172–332 m)	2488 m	0.0787	30 (30/0)	5.7
Zone 4 (>332 m)	—	—	—	2.0

Note: Numbers in parentheses represent two body-size groups of marked metamorphs: large (mean = 43.7 mm snout–vent length [SVL]) and small (mean = 39.5 mm SVL), respectively.

released prior to the next suitable night for migration within six days.

In conjunction with the encircling fence, we established arrays of 30 m long partial fences to monitor migrations to and from GB. Partial fences were constructed of 35 cm tall aluminum flashing buried 5–8 cm in the ground, with pitfall traps placed at 7.5-m intervals. Partial fences were systematically located to provide equivalent sampling effort in the cardinal directions at 90 m (n = 4; in years 2003, 2005–2007), 172 m (n = 8, all years), and 332 m (n = 7 in 2005–2007, n = 8 in 2002–2003) from the wetland edge. Prior studies at the GB encircling fence had not identified any noticeable movement corridors from the uplands into the breeding site (D. E. Scott, *personal observation*). These outer fences defined four terrestrial zones, and sampled 7.9–15.1% of the circumference at each distance (Table 1). Cohort-marked juveniles recaptured at outer fences were weighed, measured, and remarked with an individual code. Unmarked immigrating adult ambystomatids captured at outer fences in 2006 were marked by clipping a single toe on one foot that indicated the fence distance at which they were captured; in 2007 this technique was supplemented by using photos to individually identify *A. opacum*, and toe clipping to individually mark *A. talpoideum*. We summed adult first captures at the peripheral and wetland fences to estimate the breeding population size and distribution for each year of visibly mature animals that were captured headed toward GB during the species' breeding season; i.e., adults captured in buckets indicating direction of travel away from GB, perhaps toward another breeding site, were excluded from analyses, as were adults captured in the non-breeding season.

Statistical methods

Terrestrial distribution (i.e., distance from the wetland) was estimated by combining a model for the distribution, e.g., lognormal, with information about the probability of capture at each distance. We considered a variety of two-parameter models, including gamma, lognormal, normal, Weibull, and Cauchy distributions, to summarize the distribution and distance of animals around the wetland. The parameters of each model were estimated by maximum likelihood. The best-fitting model was the one with the smallest AIC statistic. The variance–covariance matrix for the estimated parameters was calculated as the negative inverse of the Hessian matrix (Efron and Hinkley 1978). The 50% and 95% quantiles of the terrestrial distribution (e.g., the distance within which 50 or 95% of the individuals are found) were calculated using the estimated parameters. A 95% confidence interval for each quantile was constructed by a parametric bootstrap, using the asymptotic distribution of the estimated parameters. The parametric bootstrap was much faster than a nonparametric bootstrap and gave essentially the same results when we computed both. Fitting the distance distributions was done using R (R Development Core Team 2009).

The details of the likelihood and probability of capture are different for juveniles and adults because the data are recorded differently for juveniles and adults. The juvenile data are summarized as the total number caught at each distance. The number of captures at a particular distance is modeled as an independent binomial random variable with N equal to the number of emigrating juveniles and Pr equal to the probability of capturing an emigrating juvenile at distance i. This probability is computed as Pr[juvenile captured at distance i] = Pr[juvenile emigrated past distance i] × Pr[capturing an animal passing distance i]. The second term is given by the proportion of the circumference comprised by all fences at this distance (Table 1). The probability of emigrating past distance i is $D_i = 1 - F(D_i \mid l, s)$, where $F(D_i \mid l, s)$ is a particular cumulative distribution function for emigration distance (e.g., lognormal, gamma) and l and s are the location and scale parameters for that distribution.

The adult data are summarized as the distance at which a presumed breeder was first captured, so the log-likelihood has a multinomial form. The probability of capture at the outer distance is the probability an adult started beyond 332 m times the probability that it was caught as it passed the 332-m fences. As with juveniles, the probability of capturing an adult as it crosses the imaginary circle at 332 m is the proportion of the circumference that is fenced. The probability that an animal started beyond 332 m is $1 - F(332 \mid l, s)$, where $F(332 \mid l, s)$ is a particular cumulative distribution function for adult immigration distance. Because adults are recorded as the distance at which they are first captured, the probability of capture at the 172-m fence is the sum of two probabilities: the probability that an adult started between 172 m and 332 m and was caught at the 172-m fences plus the probability that an adult started beyond 332 m, was not caught at the 332-m fence, but was caught at the 172-m fence. The probabilities for the 90-m and inner fences were calculated as extensions of the same argument.

We used an a priori linear contrast to test for a body condition trend of emigrating juvenile *A. opacum* recaptured at increasing distances from the wetland; body condition index was defined as the residual from the linear regression of natural log-transformed mass on natural log-transformed SVL for juveniles measured at the wetland edge ($n = 620$). A decline in wet mass per unit body length at increasing distance from the wetland could be due to a reduction in energy reserves, perhaps indicating a cost of juvenile dispersal away from the wetland. The terrestrial distribution of large- vs. small-bodied *A. opacum* metamorphs was compared using a two-way chi-square test with a P value computed by Monte-Carlo randomization or complete enumeration of the randomization distribution when the counts were small. These P values are appropriate even if cell counts are small; the tests were conducted using SAS for Windows Version 9.2 (SAS Institute 2009).

We combined our results with movement data from seven studies summarized in Semlitsch (1998) and nine more recent studies for which the mean distance traveled from a breeding site by a species/group, the sample size, and a variance estimate (SD, SE, or CV) were available. For each study we calculated the 95% quantile of distance traveled, assuming a lognormal distribution. For a lognormal distribution, the mean distance is $\exp(m + v/2)$ and the CV (mean/SD) is $\mathrm{sqrt}(\exp(v) - 1)$, where m and v are the mean and variance of log-transformed distances and sqrt is the square-root function. We computed m and v from the reported means and variances, then calculated the 95% quantile of distance traveled as $\exp(m + \mathrm{qt}(0.95, n - 1) \times \mathrm{sqrt}(v))$, where qt is the 0.95 quantile of the T distribution with $n - 1$ df. If the sample size is large, the t quantile approaches 1.645, the 0.95 quantile of a standard normal distribution.

RESULTS

Cohort characteristics of newly metamorphosed A. opacum *in 2005*

We marked 10 395 newly metamorphosed *A. opacum* at GB from 12 April to 20 May 2005. Most ($n = 10\,118$) were relatively large metamorphs from the natural wetland or the low-density enclosures. A subsample of these animals ($n = 822$) was weighed and measured (SVL $= 43.7 \pm 0.07$ mm; mass $= 2.26 \pm 0.01$ g [mean ± SE]). Remaining animals ($n = 277$), primarily from the high-density enclosures, were smaller ($n = 221$, SVL $= 39.5 \pm 0.12$ mm, mass $= 1.53 \pm 0.02$ g).

Terrestrial distribution of juveniles and adults

Juvenile A. opacum.—A total of 416 newly metamorphosed marked *A. opacum* were recaptured at outer fences from May to September 2005 (Table 1). A lognormal distribution best fit the observed numbers of captures, but a Cauchy (Lorentzian) distribution fit nearly as well (Appendix B: Table B1). Graphical comparison of the observed and expected counts indicated a good fit of the lognormal distribution. The estimated parameters for the juvenile distribution were 3.15 ± 1.54 (mean ± SD). Metamorphs congregated in Zone 1 during the four months immediately after metamorphosis, with ~8% migrating >172 m from the wetland (Fig. 1A).

Adult A. opacum.—Breeding population sizes (both sexes) across four years ranged from 961 to 3025 (Table 2). Lognormal distributions were the best fit in each year (Appendix B: Table B1). Again, graphical comparison of the observed and expected counts indicated a good fit of the lognormal distribution. One set of lognormal parameters was not appropriate for all years ($\chi^2 = 13.79$, df $= 6$, $P = 0.032$); most change occurred between 2002–2003 and 2006–2007 ($\chi^2 = 11.21$, df $= 2$, $P = 0.0037$). In 2002–2003, on average, approximately 5.2% of adults migrated to the breeding site from >332 m, 18.9% from Zone 3, 33.8% from Zone 2, and 42% from Zone 1. In 2006–2007, adults generally migrated longer distances, except that fewer (3.6%) came from Zone 4, 25.7% from Zone 3, 46.3% from Zone 2, and only 24.3% from Zone 1 (Fig. 1B).

Adult A. talpoideum.—A total of 1646 adults immigrated to GB in 2006 and 1689 in 2007 (Table 2). The lognormal model fit best; the next best distribution was a very poor fit (ΔAIC = 120). The two years had different terrestrial distributions ($\chi^2 = 14.56$, df $= 2$, $P = 0.0007$). In 2007, a greater proportion of individuals migrated longer distances than in 2006. The distribution of *A. talpoideum* in 2006–2007 differed from *A. opacum* (Fig. 1B), with adult *A. talpoideum* occurring at greater distances from the wetland (Table 2).

Distributional shift in the A. opacum *2005 cohort*

We compared the terrestrial distribution of new metamorphs in summer 2005 with animals from that cohort that matured by age 1 or 2. A distributional shift occurred as the cohort aged (juveniles to age 1, $\chi^2 = 17.92$, df $= 2$, $P = 0.00013$; age 1 to age 2, $\chi^2 = 11.15$, df $= 2$, $P = 0.0038$; Fig. 1A). Whereas 79% of the 2005 cohort inhabited Zone 1 during the summer following metamorphosis, after two years only 13% of adults from the same cohort occurred at <90 m. By age 2, 30% of adults occurred in Zones 3 and 4, compared to only 8% of newly metamorphosed juveniles that once occurred beyond 172 m.

Sex differences in terrestrial distribution

Female *A. opacum* were distributed proportionally farther from the wetland than males in 2002 and 2006

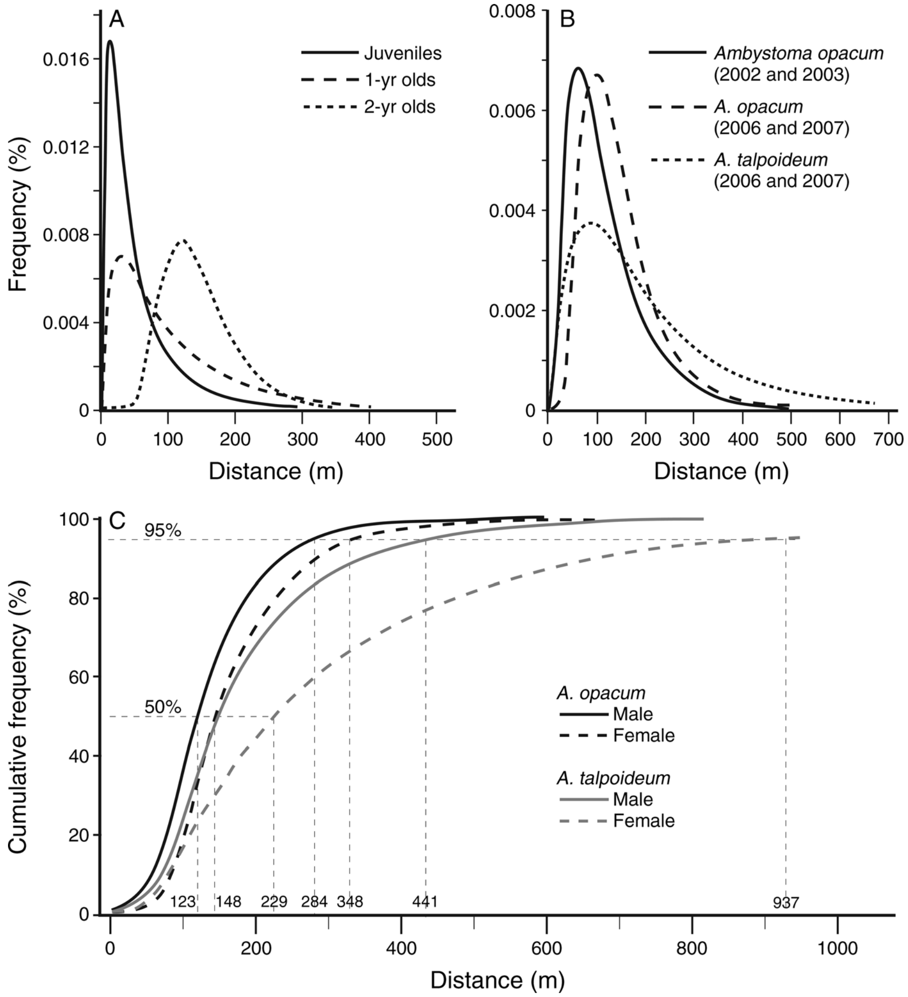

FIG. 1. Terrestrial distributions (based on lognormal models) in the upland habitat adjacent to Ginger's Bay (Aiken County, South Carolina, USA) as estimated from drift fence/pitfall trap captures at the wetland edge, 90 m, 172 m, and 332 m. (A) The 2005 cohort of *Ambystoma opacum* at Ginger's Bay as juvenile, 1-yr, and 2-yr-old adults. (B) Adult *Ambystoma opacum* and *A. talpoideum*. (C) Cumulative distribution of male and female *Ambystoma opacum* (4-yr average) and *A. talpoideum* (2-yr average), with distances at which 50% and 95% of the population occurs.

(2002, $\chi^2 = 11.89$, df = 2, $P = 0.0026$; 2006, $\chi^2 = 13.10$, df = 2, $P = 0.0014$), but not in 2003 or 2007. Averaged across years, female *A. opacum* tended to occur at greater distances than males ($\chi^2 = 20.91$, df = 2, $P < 0.0001$; Fig. 1C). Female *A. talpoideum* occurred farther than males from the wetland in both years (2006, $\chi^2 = 14.71$, df = 2, $P = 0.0006$; 2007, $\chi^2 = 10.62$, df = 2, $P = 0.0049$).

Buffer zone estimates

The radius of the buffer needed to include 50% of the migrating ambystomatids varied from 40 m from the wetland edge for juvenile *A. opacum* to 192 m for *A. talpoideum* in 2007 (Appendix C: Table C1). The 50% species averages were 133 m for adult *A. opacum* and 177 m for *A. talpoideum*. The buffer radius needed to protect 95% of animals increased to 216 m for juvenile *A. opacum*, 313 m for *A. opacum* adults, and 626 m for adult *A. talpoideum*. The uncertainty in the 95% buffer sizes is large, especially for *A. talpoideum*, but the lower bounds of the 95% confidence intervals for the *A. talpoideum* 95% buffer size exceed 450 m in both years.

Size relationships of emigrating metamorphs of A. opacum

We observed no difference ($P = 0.37$) in emigration distance related to body size (Table 1). The body condition index of newly metamorphosed salamanders exhibited a significant decline as animals traveled farther from the wetland ($F_{1,1012} = 7.44$, $P = 0.0065$, $r^2 = 0.02$).

DISCUSSION

Terrestrial distribution estimates

Our mark–recapture data for four years of adult immigration and one year of juvenile emigration allowed us to estimate terrestrial distribution patterns for this

TABLE 2. Numbers of first-captured breeding adults (males : females ratio in parentheses) at each distance and estimated terrestrial distribution of *Ambystoma opacum* (four breeding seasons) and *A. talpoideum* (two seasons) in four upland zones surrounding Ginger's Bay.

Measure	*Ambystoma opacum*				*A. talpoideum*	
	2002	2003	2006	2007	2006	2007
Number of breeders	1206 (820:386)	961 (492:469)	1652 (1025:627)	3025 (1749:1276)	1646 (1089:557)	1689 (821:868)
Captured at fence						
0 m	1149 (793:356)†	855 (442:413)	1403 (889:514)	2594 (1514:1080)	1399 (947:452)	1348 (669:679)
90 m		68 (33:35)	164 (99:65)	284 (164:120)	115 (71:44)	166 (89:77)
172 m	51 (23:28)	32 (14:18)	77 (34:43)	136 (65:71)	108 (63:45)	144 (53:91)
332 m	6 (4:2)	6 (3:3)	8 (3:5)	11 (6:5)	24 (8:16)	31 (10:21)
Estimated percentage in zone						
Zone 1 (0−90 m)	39.3	44.8	23.3	25.3	34.6	13.5
Zone 2 (90−172 m)	35.3	32.4	46.0	46.6	24.8	30.1
Zone 3 (172−332 m)	20.0	17.7	26.7	24.8	21.7	35.1
Zone 4 (>332 m)	5.3	5.1	4.0	3.3	18.9	21.3
Estimated lognormal						
Mean (male, female)	4.69 (4.22, 5.07)	4.60 (4.52, 6.67)	4.88 (4.78, 5.07)	4.85 (4.79, 4.93)	4.90 (4.76, 5.31)	5.26 (5.08, 5.44)
SD (male, female)	0.69 (0.98, 0.46)	0.74 (0.76, 0.71)	0.52 (0.48, 0.54)	0.52 (0.51, 0.51)	1.02 (0.87, 1.25)	0.69 (0.60, 0.73)

Notes: The mean and SD of the fitted lognormal distribution for each species and year are also presented (males, females). For *A. opacum*, the breeding season was primarily in the fall of the previous year; e.g., 2006 breeders immigrated in fall 2005.

† In 2002, there were no drift fences at 90 m (outer edge Zone 1); 0 m totals reflect a combination of Zones 1 and 2.

ambystomatid community. Our findings are similar to other recent studies of ambystomatid terrestrial distribution: a high proportion of the population occurs at greater-than-expected distances from the wetland breeding site (Windmiller 1996, Regosin et al. 2005, Trenham and Shaffer 2005, Gamble et al. 2006), if expectations are based on a 164-m radius to encompass 95% of the population (Semlitsch 1998).

The majority of newly metamorphosed *A. opacum* moved a short distance from the natal wetland. We found that 79% of *A. opacum* metamorphs remained within 90 m, and 50% are estimated to be within 40 m. This is consistent with estimates for juvenile *A. opacum* in Massachusetts (15–42% within 30 m; Gamble et al. 2006) and *A. maculatum* in Massachusetts (50% within 40 m; Windmiller 1996). A lognormal distribution function best describes the upland distribution of juveniles in the months immediately following metamorphosis. Because the lognormal distribution is positively skewed, the median buffer width to protect 50% of the cohort is closer to the wetland edge than it would be if emigration distance were normally distributed with the same mean and variance; the juvenile distribution has a very long tail, with just 2% of the juveniles moving beyond 332 m.

The terrestrial distribution of adults varied between species, sexes, and years, with adults generally farther from the wetland than juveniles, females farther than males, and *A. talpoideum* farther than *A. opacum*. Again, the distributions for each species and year were well fit by lognormal distributions, but the standard deviation of the adult distributions was much less than the spread of the juvenile distributions. Estimates of amphibian habitat use in the tail of the distribution are important to determine the necessary size of buffer zones. Windmiller (1996) observed that although about half of *A. maculatum* adults occur within 100 m of the breeding pond, 14–18% migrate more than 200 m away. Similarly, we estimate 23–31% of *A. opacum* adults and 40–56% of *A. talpoideum* adults migrate from distances >172 m.

Conservation plans for pond-breeding amphibians clearly must focus on both aquatic and terrestrial habitats (Windmiller 1996, Taylor and Scott 1997, Semlitsch 1998, Snodgrass et al. 2000), as well as terrestrial habitat connectivity between breeding sites (Cushman 2006). A critical component of any conservation strategy is the protection of suitable upland habitat area (Semlitsch 1998, Semlitsch and Bodie 2003). Semlitsch (1998) summarized 16 movement studies of six ambystomatid species and calculated that adults migrate an average distance of 125.3 m, and juveniles 69.6 m, from wetlands into uplands. For a normal distribution the protection of uplands to a distance of 125 m should generally protect half the population (Semlitsch 1998). A crucial question is how much of the habitat needs protection for the population to remain viable (Harper et al. 2008), as several studies of ambystomatids have noted decreased populations with increasing loss of forested habitat (e.g., Windmiller 1996, Gibbs 1998, Homan et al. 2004). If more than 50% of the population/habitat needs protection to ensure viability, then detailed knowledge of the terrestrial distribution of animals in the population is essential (Trenham and Shaffer 2005).

In recent years additional studies have expanded those summarized by Semlitsch (1998), increasing the number of distribution estimates available for species, populations, and sexes (Appendix D: Table D1). Results of these studies, particularly those based on upland trapping, reveal (1) the mean distance within which 50% of the population occurs is roughly the same for all 36 species/groups compared to the original 16 estimates (124.7 m compared to 125.3 m in Semlitsch [1998]) and (2) the distance that encompasses 95% of the population is often far greater than 164 m. For example, 620 m of uplands around a breeding site is necessary to protect 95% of adult California tiger salamanders (*A. californiense*); in a population of spotted salamanders (*A. maculatum*), approximately 28% of adults were estimated to be >200 m from the pond shore (Windmiller 1996); for blue-spotted salamanders (*A. laterale*), at least 10–12% of adults occur beyond 164 m (Regosin et al. 2005); and in this study a 313-m zone was required to encompass 95% of *A. opacum* and a 626-m zone was needed for *A. talpoideum*.

Discrepancies between the generalized 164-m distance and more recent estimates may be due to several factors. First, the size of a buffer zone needed for 95% protection is likely to vary among species, wetland, region, and other factors (Semlitsch 1998). Second, use of radiotracking or radioactive tags to follow individuals likely underestimates movement distances (Trenham and Shaffer 2005, Rittenhouse and Semlitsch 2007). In studies comparing movement distances based on individual tracking vs. trapping methods, estimates of migration distances based on upland trapping have exceeded those from individually tagged animals (Windmiller [1996] and Trenham and Shaffer [2005] vs. Trenham [2001]; this study vs. Semlitsch [1981]). In addition to possible behavioral differences between tagged and untagged animals and the short duration of many tracking studies noted by Trenham and Shaffer (2005), a subset of tagged animals is often lost to the researcher, and these lost animals are possibly ones that move greater distances (Williams 1973, Douglas and Monroe 1981, Trenham 2001).

The third reason the 164-m radius underestimates the true 95% bound is that the 164-m distance as determined in Semlitsch (1998) is the upper 95% one-sided confidence limit for the buffer radius needed to contain 50% of the population, not the buffer radius needed to contain 95% of the population. For the 22 species/groups for which we could estimate the 95% bound for adults (Appendix D: Table D1), we estimated a 50% distribution distance (± 1 SD) of 129.7 ± 57.9 m (similar to the Semlitsch [1998] mean of 125.3 ± 73.2 m), but the average distance to include 95% of the population based on our lognormal estimates was 349 ± 186 m. This distance is 185 m greater than the 164-m estimate, and 104 m larger than a univariate kernel density estimate for the 95% boundary derived from radiotracked salamanders (Rittenhouse and Semlitsch 2007). For management efforts that focus on individual wetlands/populations, an accurate depiction of the within-population terrestrial distribution is essential to estimate needed buffer zone size.

Juvenile emigration

In this study, we were unable to distinguish emigrating juvenile *A. opacum* from juveniles that might ultimately disperse to non-natal breeding sites. Juveniles may be an important dispersing stage for pond-breeding salamanders (Trenham et al. 2001, Gamble et al. 2007), and 5–9% of juvenile *A. opacum* are known to breed for the first time at non-natal wetlands (Scott 1994, Gamble et al. 2007). Although we observed ~2% of juveniles emigrate beyond 332 m, we also captured nearly 6% of known 1- and 2-yr-old survivors of this cohort returning to GB from beyond 332 m. It does not appear that all juveniles in the tail of the distribution were dispersing to another pond.

Mobility in recently transformed amphibians may be related to body size (Vasconcelos and Calhoun 2004). However, migratory success is not related to juvenile size in either *A. maculatum* or *Bufo americanus* (Rothermel 2004). In our test for effect of size on emigration distances of *A. opacum* metamorphs, ~80% of juveniles of both size classes remained in Zone 1; we observed no evidence for size-related migration differences. The decreased body condition index of animals recaptured at outer distances, which we attempted to hydrate equally before weighing, suggests there may be an energetic cost to emigration in the first months post-metamorphosis (Windmiller 1996). Energy stores at metamorphosis are strongly related to juvenile survival (Scott et al. 2007), and mortality is highest in the months immediately following metamorphosis (Rothermel and Semlitsch 2006), thus, there may be strong selection against long distance (energetically expensive) movements by juveniles. However, given our methodology, we cannot disentangle mass loss as a consequence of emigration from the use of energy stores for metabolic maintenance during the time since emergence (Scott 1994). Additionally, our analysis explained only 2% of the variance in the body condition index, perhaps because total lipids comprise only 1.4% of body wet mass (Scott et al. 2007). Experimental studies that focus on the use of energy stores during the post-metamorphic period will be necessary to determine if our observation of a reduced body condition index in animals that traveled farther from their natal site is biologically meaningful.

The cause of the outward shift in terrestrial distribution for the 2005 cohort from several months post-metamorphosis to two years later is unknown, and may reflect either differential mortality or delayed movement away from the wetland (Gamble et al. 2006, Semlitsch 2008). We did not keep the pitfall traps open from May to August in 2006, and cannot distinguish between the two possible causes.

Processes affecting terrestrial distributions

The timing of juvenile emergence, coupled with harsh post-emergence environmental conditions such as reduced upland soil moisture, may select for limited movement of juveniles away from natal ponds. For

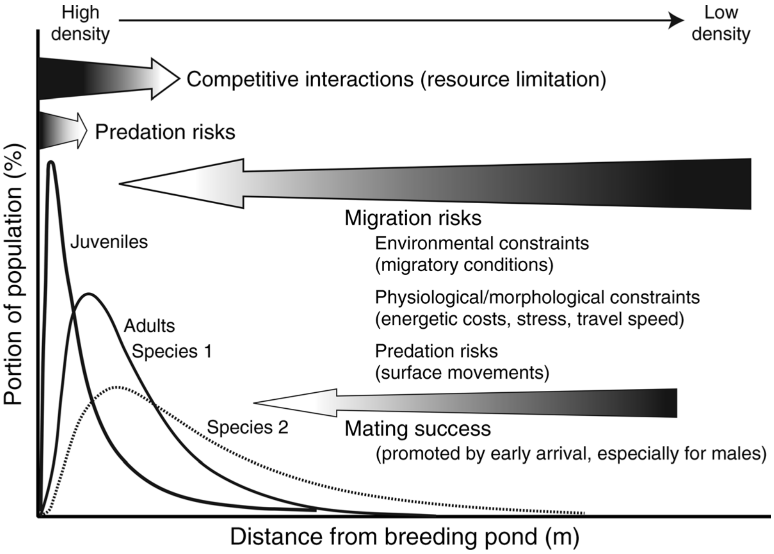

FIG. 2. Conceptual model of the opposing selective forces that shape the terrestrial distribution of ambystomatids. Shaded gradient in arrows represents the changing intensity of the selection pressure over distance. Higher levels of predation and competition near the wetland may promote settling in suitable habitat away from the wetland, whereas increased mating success, decreased migration risks, and lowered physiological costs of migrations may encourage remaining in close proximity to the breeding site.

adults, the physiological stress (Homan et al. 2003), energetic costs (Windmiller 1996) and predation risk associated with migrations may drive distributions closer to breeding habitats. Simultaneously, predation risk in and near wetlands (e.g., Greenwood 1982) likely promotes establishment of home ranges away from wetlands. Similarly, competition for limited resources (Regosin et al. 2003) would further encourage migration to greater distances and associated lower density (Gamble et al. 2006), as is suggested by the relatively sparse distributions we observed in the terrestrial habitat. Competition for burrows, with *A. opacum* aggressively defending burrows by excluding heterospecifics (Smyers et al. 2002), may account for the more distant distribution of *A. talpoideum*. The energy needs of females for egg production (Scott and Fore 1995) may require them to move farther than males to increase per capita food intake (Rittenhouse and Semlitsch 2007), but this energetic advantage may be opposed by the greater risk of longer migrations. Also, males may be selected to remain close to the breeding site so they arrive first during the breeding migrations (Scott 2005). Collectively, these processes likely shape the variability in distributions observed among life stages, species, years, and sexes (Fig. 2).

Conservation implications

Ambystomatid salamanders need suitable terrestrial habitat adjacent to breeding sites. Our results, combined with other recent studies and reanalysis of previous data, show that the area required to encompass 95% of the population is larger than previously thought. Before we can understand the potential impact of terrestrial habitat loss around wetlands to amphibian populations and design appropriate management strategies, we must first know the spatial distribution of animals (Trenham and Shaffer 2005). Knowing the distribution in undisturbed habitat, we can better predict how increased disturbance of upland habitats, including climate change impacts on wetland hydroperiods and connectivity (Walls et al. 2013), may influence amphibian distributions, survival, and population viability (Homan et al. 2004, Trenham and Shaffer 2005, Harper et al. 2008). Individuals that stay in low quality habitat, such as clear-cuts, incur reduced growth and survival (Rothermel and Semlitsch 2006). However, if individuals choose to retreat to more suitable forest habitat (Todd et al. 2009), the higher resulting densities may produce similar negative effects on vital rates, including fecundity. A relatively modest reduction in juvenile/adult annual survivorship (e.g., from 70% to <60%) may be sufficient to induce local extinction in the absence of increased immigration rates or other compensatory effects (Taylor and Scott 1997). More information on the behavioral response of ambystomatids to habitat degradation, effects of terrestrial crowding in relation to habitat loss, and their consequences for population viability is needed.

Our finding that the area needed to protect 95% of a population extends far beyond 164 m has obvious implications for forest management decisions and the design of reserves: for a 1-ha wetland, the required terrestrial buffer area is approximately 3.5 times greater than the 164-m radius estimate (50.5 compared to 14.2 ha). In some instances the protection of an entire core habitat may be unnecessary because a species does not use all the habitat elements (e.g., wood frogs; Baldwin et al. 2006). However, for the ambystomatid salamander group, conservation of only specific habitat elements within a larger core area is unlikely to achieve population protection due to the widespread dispersion of individuals throughout available terrestrial habitat (but see Windmiller 1996). The use of best development practices, as proposed by Calhoun et al. (2005), offers promise, but with the caveat that for many *Ambystoma* species the core conservation zone at some wetlands may need to extend to 500 m or beyond, especially considering the longer distances traveled by females (Faccio 2003, Regosin et al. 2005, McDonough and Paton 2007). Because frogs are generally distributed farther from breeding sites than salamanders, a protected area that is sufficient to protect many salamander species may be insufficient to maintain viable frog populations (Rittenhouse and Semlitsch 2007).

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SUPPLEMENTAL MATERIAL

Appendix A

Locations of the encircling drift fence/pitfall traps, and partial fences at 90, 172, and 332 m from the Ginger's Bay wetland in Aiken County, South Carolina, USA (*Ecological Archives* E094-233-A1).

Appendix B

AIC values for model fit comparisons of the terrestrial distributions of adult and juvenile ambystomatids (*Ecological Archives* E094-233-A2).

Appendix C

Estimated buffer radii that contain 50% or 95% of the juvenile *Ambystoma opacum*, adult *A. opacum*, or adult *A. talpoideum* around Ginger's Bay (*Ecological Archives* E094-233-A3).

Appendix D

Summary of terrestrial mean migration distances (±SD) for eight ambystomatid species (*Ecological Archives* E094-233-A4).