

Consequences of forest fragmentation for juvenile survival in spotted (*Ambystoma maculatum*) and marbled (*Ambystoma opacum*) salamanders

B.B. Rothermel and R.D. Semlitsch

Abstract: We compared demographic traits of postmetamorphic salamanders among old fields, forest interior, and edge habitats over 2 years. Recently metamorphosed spotted salamanders (*Ambystoma maculatum* (Shaw, 1802)) and marbled salamanders (*Ambystoma opacum* (Gravenhorst, 1807)) were individually marked, added to terrestrial enclosures, and recaptured in pitfall traps. Proportion known alive in the fields was <5% by the first fall and declined to 0% for both species in the 2nd year. In forested enclosures, significantly more *A. opacum* (mean 38.5%) and *A. maculatum* (mean 16.7%) survived until the first fall and several individuals of each species attained sexual maturity. Mean proportion known alive was approximately two times higher in *A. opacum* than in *A. maculatum*, perhaps because of an advantage of earlier metamorphosis in *A. opacum*. Our results indicate that the first few months in the terrestrial environment is a critical period which determines survival between metamorphosis and first reproduction. Juveniles that weighed more initially had greater chances of surviving this period. We found no evidence that proximity to forest edges incurred fitness costs in terms of reduced growth or survival for juvenile ambystomatids. Because no juveniles survived to maturity in fields, breeding sites surrounded by non-forested habitat may be population sinks for these species.

Résumé : Nous avons comparé pendant 2 ans dans des habitats de champ abandonné, de milieu forestier et de lisière les caractéristiques démographiques de salamandres ayant complété leur métamorphose. Des salamandres maculées (*Ambystoma maculatum* (Shaw, 1802)) et marbrées (*Ambystoma opacum* (Gravenhorst, 1807)) récemment métamorphosées ont été marquées individuellement, mises dans des enclos terrestres et capturées de nouveau dans des pièges à fosse. Dans les champs, la proportion de salamandres trouvées vivantes est <5 % le premier automne et elle est réduite à 0 % durant la seconde année chez les deux espèces. Dans les enclos forestiers, des proportions significativement plus élevées d'*A. opacum* (moyenne de 38,5 %) et d'*A. maculatum* (moyenne de 16,7 %) survivent jusqu'au premier automne et plusieurs individus des deux espèces atteignent la maturité sexuelle. La proportion moyenne de salamandres trouvées vivantes est environ deux fois plus élevée chez *A. opacum* que chez *A. maculatum*, peut-être à cause d'un avantage relié à la métamorphose plus hâtive chez *A. opacum*. Nos résultats indiquent que les quelques premiers mois passés en milieu terrestre sont une période critique qui détermine la survie de la métamorphose à la première reproduction. Les jeunes qui, au départ, ont une masse plus élevée ont une probabilité plus grande de survivre à cette période. Nous ne trouvons aucune indication qu'une proximité des lisières de la forêt entraîne chez les jeunes ambystomatidés des coûts reliés à la fitness en ce qui a trait à la réduction de la croissance ou de la survie. Parce qu'aucun jeune n'a survécu jusqu'à la maturité dans les champs, les sites de reproduction entourés d'habitats non forestiers peuvent représenter des puits démographiques pour ces espèces.

[Traduit par la Rédaction]

Introduction

The development of effective conservation strategies for amphibians requires an understanding of how demographic parameters vary in disturbed versus undisturbed habitats. Amphibian populations have been declining at an alarming rate over the past few decades (Alford and Richards 1999; Houlahan et al. 2000; Green 2003; Stuart et al. 2004).

Although the loss or degradation of suitable habitat is a well-documented and widespread threat to the long-term viability of amphibian populations (Davidson et al. 2001; Dodd and Smith 2003), there is a paucity of information on the responses of amphibians to landscape modification, especially for the terrestrial life stages of pond-breeding amphibians. Estimates of basic demographic parameters in relation to land use for mole salamanders in the family Ambystomatidae are especially scarce owing to the fossorial habits of juveniles and adults.

This is in contrast to the extensive body of literature on factors influencing success in the aquatic larval stages, which has demonstrated that density dependence is a major factor regulating population dynamics (Wilbur and Collins 1973). One consequence of high larval density is smaller size at metamorphosis, which has important carry-over effects on demographic traits of subsequent life stages. These include smaller size at maturity in anurans (Smith 1987; Berven 1990) and salamanders (Semlitsch et al. 1988; Scott

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1994). Smaller size at maturity reduces fecundity in salamanders, as body size and clutch size are positively correlated (Kaplan and Salthe 1979; Semlitsch 1985; Scott 1994). Smaller individuals may also take longer to reach maturity (Smith 1987; Semlitsch et al. 1988; Berven 1990; Scott 1994). Finally, smaller size at metamorphosis sometimes leads to lower survival to first reproduction (Berven 1990; Goater 1994; Pechmann 1994; Scott 1994), but the mechanisms for this effect are poorly understood.

Ambystomatid salamanders spend the vast majority of their lives in the terrestrial environment adjacent to breeding sites (Semlitsch 1998). Thus, in situations of extreme habitat fragmentation, a large proportion of the population may find itself occupying altered and perhaps suboptimal terrestrial habitats, with unknown consequences for population dynamics. For many species of salamanders and frogs, the juvenile stage lasts 2–3 years and most growth occurs in the terrestrial phase (Werner 1986; Goater 1994). Because ambystomatids are long-lived, studies on the order of tens of years are required to gain insight into the factors regulating population dynamics (Pechmann et al. 1991). Such long-term studies of California tiger salamanders (*Ambystoma californiense* Gray, 1853; Trenham et al. 2000) and marbled salamanders (*Ambystoma opacum* (Gravenhorst, 1807); Taylor and Scott 1997) suggest that population dynamics may be highly sensitive to variation in postmetamorphic survival. Ecological sensitivity analyses based on data for other pond-breeding amphibians also indicated that postmetamorphic survival rates have the strongest influence on local population dynamics (Biek et al. 2002; Vonesh and de la Cruz 2002).

The primary objective of our study was to compare survival rates of juveniles of two salamander species among habitats differing in degree of alteration. We obtained estimates of demographic parameters in different habitats by raising juvenile spotted salamanders (*Ambystoma maculatum* (Shaw, 1802)) and *A. opacum* in terrestrial enclosures in old fields, interior forest, and edge habitats. The placement of enclosures inside forest edges allowed us to test for potentially negative edge effects, which have been shown to influence the persistence of other taxa such as forest-dependent songbirds in fragmented landscapes (e.g., Donovan et al. 1997; Howell et al. 2000). deMaynadier and Hunter (1999) found lower abundance of spotted salamanders within 20–30 m of a forest edge in Maine, suggesting edge effects may be important for ambystomatids. Raymond and Hardy (1991) invoked edge effects as a possible explanation for lower abundance of ambystomatids at a pond 156 m from a clearcut, although abiotic influences rarely extend that far (Murcia 1995). Finally, Weyrauch and Grubb (2004) found woodlot edge to area ratio was the most important landscape variable determining salamander species richness in Ohio and recommended maintaining large tracts of forest to conserve ambystomatid salamander populations.

We hypothesized that juvenile success would differ among habitats, such that survival and growth would be lowest in old fields, intermediate in edge habitats, and highest in interior forest. Alternatively, juvenile success might differ only between forest and non-forest habitat, such that survival and growth would be low in fields and high in forest, regardless of proximity to edges. In addition, by com-

paring the responses of two species, our study addressed whether conservation strategies for amphibians need to be species-specific or can be aimed at higher taxonomic levels. Although marbled and spotted salamanders are both forest-associated, we predicted that spotted salamanders would show stronger responses to habitat differences, experiencing higher mortality in fields and edge habitats than marbled salamanders. Several landscape-level studies suggest that spotted salamanders are sensitive to forest fragmentation, based on their absence in highly fragmented landscapes and significant association with proximity to forest and amount of forest cover in moderately fragmented landscapes (Gibbs 1998a; Kolozsvary and Swihart 1999; Guerry and Hunter 2002; Weyrauch and Grubb 2004).

Materials and methods

Study design

Twelve 6 m × 3 m terrestrial enclosures were constructed in April and May of 2001 at the University of Missouri's 923 ha Baskett Wildlife Research Area in Boone County, Missouri. Four enclosures were placed in each of three habitat types: interior forest (>75 m inside a forest edge); edge (<20 m inside an existing forest edge); and old fields (>30 m from nearest forest edges). Although random placement of enclosures would have been desirable from an experimental design standpoint, placement was constrained by the availability of sites meeting certain criteria (e.g., forest overstory dominated by hardwoods, similar soil type and elevation, slope <10%, minimum distance of 50 m between enclosures).

Each enclosure was divided down the middle to form paired 3 m × 3 m enclosures (24 total). The perimeter of each enclosure was trenched mechanically to a depth of 45–60 cm. Aluminum flashing (91 cm wide) was secured to short pieces of angle iron on the inside corners and supported by wooden stakes on the outside. Seams between overlapping pieces of flashing were sealed using silicon caulk and aluminum tape, creating a smooth surface. Finally, soil was packed along the bottom edge to ensure a tight seal and the trenches were completely backfilled by hand. When completed, the enclosure walls extended 30–40 cm below ground and 50–60 cm above ground. To restore ground cover inside the enclosures, we added leaf litter and woody debris from an area of adjacent undisturbed ground that was equivalent to the area disturbed by trenching. At field enclosures, we transplanted clumps of grass and other vegetation into the disturbed, relatively bare areas along the inside edges of the enclosures.

Study species

Spotted salamanders are common in central Missouri, whereas marbled salamanders are more patchily distributed (Johnson 2000). Adults of both species prefer fishless, temporary ponds in or adjacent to forest for breeding, but they breed at different times (Petranka 1998). Marbled salamanders breed in autumn. Females deposit a clutch of eggs in a dry pond basin or at the edge of a pond and stay with the clutch for some time. Hatching is triggered when late fall or winter rains fill the pond, inundating the nest. The larvae then overwinter in the pond. Spotted salamanders, on the

other hand, migrate to ponds to breed when temperatures warm slightly in late winter or early spring (Sexton et al. 1990). Marbled salamander larvae metamorphose and begin leaving ponds several weeks to months earlier than spotted salamanders. Postmetamorphic spotted salamanders typically require from 2 to 3 years and marbled salamanders from 1 to 5 years to reach sexual maturity (Petranka 1998).

We collected approximately 22 egg masses of spotted salamanders from a forested pond at the Baskett Wildlife Research Area in Boone County, Missouri, on 17 and 19 March 2001. The egg masses were transferred to polyethylene cattle tanks at the University of Missouri's Research Park in Columbia, Missouri, where they hatched between 10 and 26 April. When larvae were several days old, we transferred them to 2.4 m diameter cattle tanks at the same facility. Each tank had been filled with approximately 2000 L of water in early March and stocked with leaf litter (2 kg/tank) and zooplankton collected from several sites within the Baskett Area. Tanks were initially covered with mesh lids to prevent colonization by predaceous insects (e.g., dragonflies, beetles), but lids were removed once salamander larvae had reached a larger size. We stocked 19 tanks with a total of 1466 spotted salamander larvae (at densities of 0.03–0.04 per L).

We obtained marbled salamander larvae from a forested pond at the Daniel Boone Conservation Area in Warren County, Missouri, on 21 March 2001. The larvae were still small (<30 mm total length) and had not yet developed hind limbs (less than stage 49; Donovan 1980). They were transferred immediately to the University of Missouri's Research Park and added to three cattle tanks, prepared as described above ($n = 62$ per tank, for a density of 0.03 per L). Our use of animals was reviewed and approved by the University of Missouri's Animal Care and Use Committee and all animals were cared for in accordance with ASIH *Guidelines for Use of Live Amphibians and Reptiles in Field and Laboratory Research* (2nd ed., Herpetological Animal Care and Use Committee, American Society of Ichthyologists and Herpetologists).

We checked tanks every morning for metamorphosed individuals. Marbled salamander larvae metamorphosed between 11 May and 11 June. Spotted salamander started metamorphosing on 31 May and larvae were still present when tanks were drained on 15 July. Because of the variation in dates of metamorphosis, we kept recently metamorphosed salamanders in terrestrial holding tanks outdoors until we could mark and add them to the enclosures. Holding tanks were 1.8 m diameter cattle tanks filled with 20–25 cm of leaf litter, placed in the shade, and covered with mesh lids.

We removed salamanders from the holding tanks and marked them on 27–29 May (marbled salamander) and 22–25 June (spotted salamander). Salamanders were first anesthetized in MS-222 (concentration of 1 g per 500 mL for 1.5–2 min) and measured. As a close approximation of snout–vent length (SVL), we measured from the tip of the snout to the posterior insertion of the hind limb to the nearest millimetre. We then gave each salamander within an experimental enclosure a unique mark by clipping one toe on the left hind foot and two adjacent toes on the right hind foot. Because of the unreliability of toe clips as a long-term

marking technique, we also marked each animal with visible implant elastomer (VIE; Northwest Marine Technology, Shaw Island, Washington). The still-anesthetized salamanders were given a unique mark by combining four elastomer colors with three body positions. The order of marking was based on ID so that all 12 salamanders of each species receiving the same ID (but destined for 24 different enclosures) were marked before proceeding to the next batch. This ensured that differences in time spent in the laboratory following marking were evenly distributed among enclosures. Once the study was underway and juveniles acquired their adult pigmentation (within 1–2 months following metamorphosis; Petranka 1998), we used photographs of their natural markings as another form of identification. The use of redundant marking systems allowed us to verify the identity of every recaptured individual despite the frequent occurrence of toe regeneration and loss of one or more elastomer marks.

All juveniles survived the minimum 24 h post-marking observation period. Marked individuals of each species of a given ID were haphazardly distributed to 24 containers, which were then randomly assigned to enclosures. On the day of release, salamanders were weighed in the laboratory, then transported to the study area in coolers. Groups of salamanders were added to all enclosures within a 1.5 h period in the evening. We added marbled salamanders ($n = 144$) to the enclosures on 30 May and spotted salamanders ($n = 144$) on 28 June 2001.

The initial density of each half-enclosure was 1.3 salamanders per m^2 . Because of the difficulty of locating ambystomatid salamanders during the nonbreeding season, there is very little information on natural terrestrial densities, which vary widely depending on timing of sampling, habitat quality, and population sizes. Pechmann (1995) stocked juvenile marbled salamanders and mole salamanders (*Ambystoma talpoideum* (Holbrook, 1838)) in terrestrial enclosures at either 0.31 per m^2 (low-density treatment) or 0.62 per m^2 (high-density treatment), levels consistent with estimates of natural densities at his site in South Carolina. In another study in South Carolina, juvenile mole salamanders stocked at a density of 0.8 per m^2 exhibited good survival and growth rates (Chazal and Niewiarowski 1998). Because Pechmann (1995) and Chazal and Niewiarowski (1998) failed to detect negative density-dependent effects in the terrestrial stages of marbled and mole salamanders, we felt it was reasonable to use a higher density than was used in either of these studies.

Recapture techniques and data collection

Pitfall traps were installed in three corners of each 3 m × 3 m half-enclosure in September of 2001. The traps consisted of 20 cm sections of 15 cm diameter PVC pipe capped with aluminum window screening on the bottom (Crawford and Kurta 2000) and buried so that the open end was level with the surface of the soil and the trap was in contact with the wall of the enclosure. To provide cover and moisture for captured salamanders, we placed leaves in traps in the forest and edge enclosures and sponges in traps in field enclosures. Starting in September 2001, we opened traps periodically during the spring and fall, when salamanders were most likely to be active. The inclusive dates of

each trapping session were 16 September – 24 October 2001 (10 days total), 8 March – 14 May 2002 (50 days), 17 September – 19 December 2002 (30 days), and 2 February – 11 June 2003 (55 days). At all other times, the traps were kept closed with tight-fitting plastic caps.

As in previous studies (e.g., Pechmann 1995), we assumed that salamanders would initiate their breeding migration upon reaching sexual maturity, thereby ensuring capture in pitfall traps. By using relatively small enclosures, we were also able to capture immature individuals to assess their growth and survival throughout the juvenile stage. Captured salamanders were brought back to the laboratory, where they were identified, photographed as needed, measured (tip of snout to posterior end of cloaca, to the nearest 1.0 mm), and weighed (live mass to nearest 0.001 g). Immature individuals were returned to their enclosures within 24 h of capture. Mature individuals (i.e., possessing swollen cloaca in males, ova visible by candling in females; Pechmann 1994) were euthanized in chloroform and preserved in 4% formalin on the day of capture. All salamanders captured in spring of 2003 were removed, euthanized, and preserved upon their first capture. All surviving salamanders that were captured and preserved in fall 2002 and spring 2003 were dissected to assess the stage of reproductive development and to determine sex, in the absence of external secondary sex characteristics (details in Rothermel 2003).

The study was terminated after 2 years. In May 2003, we searched each enclosure for surviving individuals by carefully removing litter and herbaceous ground cover from each enclosure and searching for potential burrow entrances. We excavated (by hand) all openings or crevices in the soil surface larger than 1 cm in diameter. Following this intensive search, pitfall traps were left open and checked after every rain for 24 days to capture remaining survivors.

Characterization of habitat and environmental conditions

Daily precipitation and temperature records for the summer of 2001 were obtained from the weather station at Columbia Regional Airport, which is located less than 7 km from the study area (NOAA, National Climatic Data Center, Asheville, North Carolina). In August of 2001, we installed temperature data loggers (HOBO H8, Onset Computer Co., Bourne, Massachusetts) on 1 m tall wooden posts in half the enclosures (two in each habitat type). We installed underground soil moisture sensors (Watermark, Irrometer Co., Riverside, California) in these same six enclosures in April of 2002 and took soil moisture readings on days when traps were opened and checked. To compare soil moisture inside versus outside enclosures, we installed two additional soil moisture sensors in undisturbed habitats adjacent to one forest enclosure and one field enclosure. We found no significant differences in monthly mean, maximum, or minimum soil moisture (Student's *t* tests, all $p > 0.50$) measured inside versus outside the enclosures. We also sampled the top 10–12 cm of soil in each enclosure in September of 2002 and submitted the samples to the University of Missouri's Soil Test Laboratory for determination of pH and other chemical characteristics.

In fall of 2002, we recorded the genus and diameter at breast height (DBH) of all live and dead standing trees

greater than 2 cm DBH within a circular, 0.04 ha plot centered on each enclosure (similar to McLeod and Gates 1998). We measured canopy cover, ground cover, and leaf litter depth at 2.5 m intervals along four transects originating at the center and intersecting the corners of the enclosure. At each sampling point along the transect, we used a densitometer (Geographic Resource Solutions, Arcata, California; Barbour et al. 1999) to record presence or absence of tree canopy and presence and type of ground cover (woody vegetation <1.5 m tall, grasses, other herbaceous vegetation, woody debris, leaf litter, bare soil, moss, exposed rock). These measurements were converted to percent values based on the total number of measurements taken at each enclosure ($n = 20$). We also counted the number of logs (>0.5 m long and >10 cm diameter) intersected by the transects and the number of shrubs (<1 m tall) within 1 m of the transects.

Analyses

We conducted all analyses using SAS[®] version 8 (SAS Institute Inc. 1999). All analyses of variance (e.g., ANOVA, ANCOVA, MANOVA) were conducted using the general linear model procedure (PROC GLM). We used enclosure means in the analyses, because the enclosures were the true experimental units; individuals within enclosures cannot be considered statistically independent (Hurlbert 1984). In some instances there was only one observation per enclosure, so we used the single value.

Because we could not capture every surviving salamander in every trapping session, our estimates of survival represent the "proportion known alive", i.e., the proportion of salamanders originally released into each enclosure that was known to be alive in a given season. For individuals that went undetected in one season but were later recaptured, we retroactively adjusted the enclosure survival estimates to count them as alive in the previous season(s). We also restricted our statistical analysis of survival to the period from addition of salamanders to enclosures until the first trapping session in fall of 2001. The estimates of survival as of fall 2001 were more reliable, because it was highly improbable that individuals that survived the first summer could have evaded capture in all subsequent trapping sessions. Furthermore, most mortality occurred during the first few months of the study.

We used ANOVA to test the effects of habitat, species, and their interaction on proportion known alive in each enclosure to fall of 2001. Proportion surviving was arcsine square-root transformed prior to analysis to meet assumptions of heterogeneity of variances and normality (Snedecor and Cochran 1989). For significant effects in the ANOVA, we performed multiple comparisons using a Student–Newman–Keuls test (Underwood 1997) to determine which factor levels differed.

We also used logistic regression (PROC GENMOD) to determine whether initial mass (i.e., size at metamorphosis) influenced individual odds of survival. In this case, survival refers to whether individuals were known to be alive in fall 2001 based on recapture in at least one trapping session following addition to the enclosures. We calculated likelihood ratio tests for each coefficient (Allison 1991) to evaluate the effects of species and size on the binary response variable, survived or not until fall of 2001, for all salamanders

added to the enclosures ($n = 288$). Separate regressions were performed using initial mass and initial SVL as the explanatory variable.

We used data from the fall of 2002 (15–17 months post metamorphosis) to test the effects of species, habitat, and their interaction on growth. Although only a few individuals had reached maturity by fall of 2002, body size in this season could be considered representative of size at maturity, which is an important trait affecting fitness (Semlitsch et al. 1988; Scott 1994). We conducted separate ANCOVAs on percent gain in mass and percent gain in length (versus initial size) with density (number known alive) as the covariate. Effects were evaluated based on Type III sums of squares (SS) and a significance level of $\alpha = 0.10$.

We used repeated-measures ANOVA to test for differences in air temperature and soil moisture across habitat types. We used Type I SS as the basis for F tests in these ANOVAs because there was an equal number of samples within habitats ($n = 2$) in each year. When there was a significant habitat effect, we conducted post hoc pairwise contrasts.

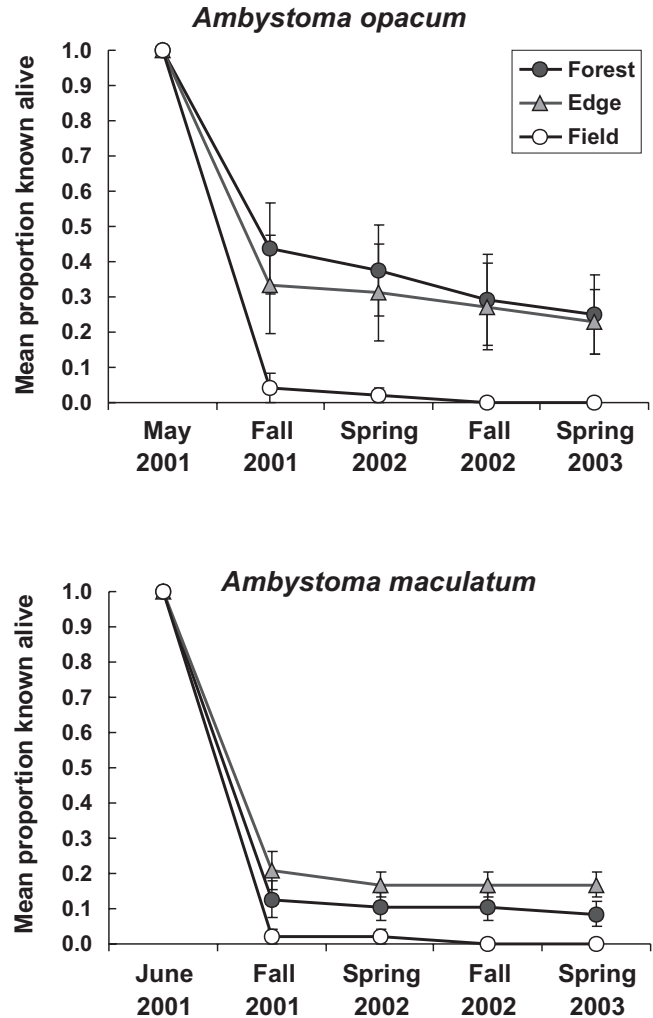
Results

Because the study was terminated before all salamanders attained maturity, an important question is whether all surviving individuals were recaptured, allowing accurate determination of survival rates. For marbled salamanders, the number of captures of new (alive but previously undetected) individuals decreased rapidly with each subsequent trapping session; only 3 of 27 (11.1%) individuals captured in spring of 2002 were previously undetected. By fall of 2002, recaptures made up 100% of the captures. In contrast, 5 of 13 (38.5%) spotted salamanders captured in fall of 2002 were previously undetected individuals. None of the salamanders captured in the fourth trapping session, however, had gone undetected in previous sessions, indicating that detection probabilities over the entire study were high. The complete capture histories of individual salamanders are provided as supplementary data (Table S1).³

There were seven instances of trespass, in which a salamander was captured on the wrong side of its enclosure, indicating that it had moved under or over the dividing wall separating the two halves of the enclosure. In all cases, the trespass occurred prior to the first capture of that individual, implying the ability to breach enclosure walls was size-related. Because the two edge and three forest enclosures with trespassing had average or higher recapture and survival rates, we had no reason to think that they were especially “leaky” and thus retained them in our analyses.

Most mortality in enclosures occurred during the first summer post metamorphosis. Proportion known alive in fall of 2001 varied from 8.3% to 33.3% for spotted salamanders and from 8.3% to 66.7% for marbled salamanders (Fig. 1). Estimates of survival for fall of 2001 are more reliable than for later time periods, for two reasons. First, we permanently removed several mature individuals of both species from the enclosures in fall of 2002. These individuals were counted as “alive” in spring of 2003 in the survivorship curves pre-

Fig. 1. Mean (\pm SE) proportion known alive of juvenile spotted salamanders (*Ambystoma maculatum*) and marbled salamanders (*Ambystoma opacum*) in terrestrial enclosures in interior forest, edge, and old-field habitats from June 2001 to 2003. Proportion known alive in fall of 2001 differed significantly among habitats ($p = 0.0051$) but not between species ($p = 0.1183$).



sented in Fig. 1. Secondly, some surviving individuals may have gone undetected in spring 2003 despite extensive efforts to capture all remaining survivors. Two spotted and five marbled salamanders were found by excavating burrows, rather than pitfall trapping, during the search of enclosures in spring 2003. Three additional marbled salamanders went undetected in this search and were captured either in pitfall traps in June 2003 ($n = 2$) or when preparing enclosures for another study in June 2004 ($n = 1$). All of these animals were in edge or forest enclosures.

Differences in survival between habitats

Proportion known alive in the first fall differed significantly among habitats (ANOVA; $F_{[2,18]} = 7.18$, $p = 0.0051$). Specifically, proportion known alive was significantly

³Supplementary data for this article are available on the journal Web site (<http://ejz.nrc.ca>) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5043. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

higher in forest and edge enclosures than in field enclosures (Fig. 1), but did not differ between forest and edge enclosures. No salamanders were ever recaptured in three of the four field enclosures. In addition, no marbled salamanders were ever recaptured in one edge enclosure and no spotted salamanders were recaptured in one forest enclosure.

Differences in survival between species

Although proportion known alive did not differ significantly between species ($F_{[1,18]} = 2.69$, $p = 0.1183$), mean proportion known alive of marbled salamanders was 3.5 times greater than that of spotted salamanders in forest and 1.6 times greater than that of spotted salamanders in edge enclosures (2.3 times greater overall; Fig. 1). There was no habitat \times species interaction ($F_{[2,18]} = 1.20$, $p = 0.3233$). The higher survival of marbled salamanders may have been due to milder weather conditions at the time of their release. Marbled salamanders were released on a day with rain, and more than 13 cm of precipitation fell in the 2-week period following their release. There was no rain on the day spotted salamanders were released, and only 6 cm of precipitation fell during the 2-week period following their release. Spotted salamanders also had to contend with higher mean daily maximum temperatures following their release (30.5 versus 26.0 °C for marbled salamanders).

Effects of size on survival

Juveniles that were large in terms of initial mass had significantly greater odds of surviving the first summer ($\chi^2_{[1]} = 4.91$, $p = 0.0268$) than smaller individuals. Spotted salamanders that survived the first summer were 9.3% (0.075 g) larger, on average, than those that did not (Fig. 2). For marbled salamanders, survivors were only 2.2% (0.016 g) larger, on average. Surviving individuals did not differ significantly in terms of initial SVL ($\chi^2_{[1]} = 2.65$, $p = 0.1035$). Despite the larger initial size of spotted salamanders, they were less likely to survive than marbled salamanders ($\chi^2_{[1]} = 15.30$, $p < 0.0001$), perhaps because of the difference in weather conditions described above. Differences in initial size could not have contributed to the observed differences in proportion known alive among enclosures, because mean initial mass did not differ among enclosures (enclosure: $F_{[11,275]} = 0.58$, $p = 0.8474$; species: $F_{[1,275]} = 39.02$, $p < 0.0001$).

Juvenile growth and size at maturity

Percent gain in mass and length as of fall of 2002 did not differ between edge and forest interior habitats, and there were no significant species or habitat \times species effects on growth (all $p > 0.1374$). In addition, growth in terms of mass and length were not affected by the covariate, density of known survivors ($F_{[1,9]} = 0.13$, $p = 0.7236$ and $F_{[1,9]} = 0.68$, $p = 0.4313$, respectively).

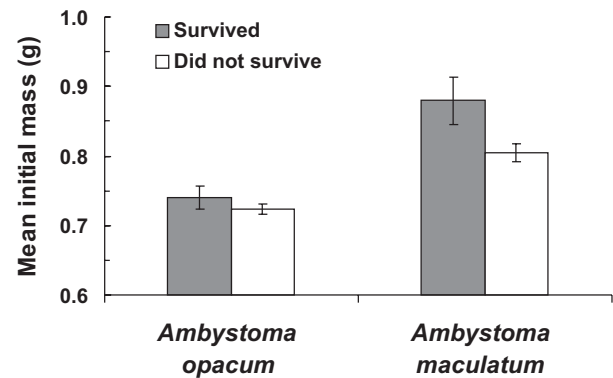
Some individuals of both species reached sexual maturity by the second fall. We captured three mature male spotted salamanders with swollen cloacae in the fall of 2002. They averaged 70 mm SVL and 8.0 g in mass. None of the female spotted salamanders in our enclosures attained maturity during their 2nd year, although all the females examined by dissection in spring 2003 had at least two sets of maturing

ova and would have been capable of breeding in spring of 2004. We also captured three mature male marbled salamanders (averaging 60 mm SVL and 5.2 g) in fall of 2002. We did not see mature ova in any of the other individuals examined by candling, although the dark pigmentation of marbled salamanders made it difficult to discern internal organs. A higher proportion of salamanders in forest enclosures attained reproductive maturity than did in edge enclosures (29.4% versus 11.1%, respectively), but the small sample sizes precluded meaningful statistical analysis.

Microhabitat characteristics and environmental conditions

During summer, mean daily temperatures in the field enclosures were 1–3 °C higher than those in edge and forest enclosures. There was a significant effect of habitat on the mean daily maximum temperatures in summer ($F_{[2,3]} = 45.84$, $p = 0.0056$). Mean daily maximum temperatures in the fields were 6–10 °C higher than those in edge and forest enclosures, resulting in significant pairwise differences (Table 1). Pough and Wilson (1970) determined a critical thermal maximum of 39.7 °C for recently metamorphosed spotted salamanders; between late June and early September of 2002, maximum temperatures met or exceeded this value in field enclosures on more than 30 days. In winter, there were no differences in mean daily maximum temperature ($F_{[2,3]} = 0.67$, $p = 0.5753$) or mean daily temperature difference across habitats ($F_{[2,3]} = 2.77$, $p = 0.2085$). Mean daily minimum temperatures also did not differ across habitats in winter ($F_{[2,3]} = 2.32$, $p = 0.2465$; Table 1). Although mean temperatures of edge enclosures were intermediate between forest and field values (Table 1), individual edge enclosures sometimes experienced more extreme temperatures than either forest or field enclosures. Mean soil moisture in late summer did not vary significantly according to habitat ($F_{[2,3]} = 1.35$, $p = 0.3822$), although forest enclosures tended to have drier soils (Table 1). Minimum soil moisture did not differ among habitats in early spring ($F_{[2,3]} = 1.69$, $p = 0.3225$) or in summer ($F_{[2,3]} = 1.60$, $p = 0.3369$).

Characteristics of the soils and vegetation varied among enclosures in different habitats (details in Rothermel 2003). Soils in forest enclosures tended to have the lowest pH and



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Table 1. Means (\pm SD) of air temperature and soil moisture across habitats and seasons.

	Season	Forest	Edge	Field
Daily temperature ($^{\circ}$ C)*				
Maximum	Summer 2001	29.2 \pm 0.5a	30.3 \pm 1.1a	38.3 \pm 1.5b
	Summer 2002	28.8 \pm 0.0	28.8 \pm 1.6	36.6 \pm 0.6
Minimum	Winter 2001–2002	-1.8 \pm 0.4	-2.0 \pm 0.0	-2.2 \pm 0.3
	Winter 2002–2003	-8.0 \pm 0.7	-8.7 \pm 0.4	-9.1 \pm 0.3
Difference	Winter 2001–2002	15.7 \pm 0.1	16.3 \pm 1.9	18.5 \pm 1.3
	Winter 2002–2003	13.0 \pm 0.4	13.7 \pm 1.8	15.6 \pm 0.7
Monthly soil moisture (centibar) [†]				
Mean	Summer 2002	127.2 \pm 24.0	78.3 \pm 23.9	96.0 \pm 35.1
	Spring 2003	5.8 \pm 2.1	5.6 \pm 1.7	6.4 \pm 3.2
Minimum	Summer 2002	166.2 \pm 33.3	109.5 \pm 38.7	154.5 \pm 48.7
	Spring 2003	6.3 \pm 2.1	6.3 \pm 1.5	7.5 \pm 4.1

Note: Mean daily maximum temperature was the only variable that differed significantly among habitats according to repeated-measures ANOVA.

*Year is the repeated measure; different letters indicate significant differences based on pairwise contrasts ($p < 0.005$, $df = 1,3$).

[†]Month is the repeated measure; note that lower values indicate higher soil moisture. Values between 0 and 10 centibars (1 bar = 100 kPa) indicate saturated soils.

Table 2. Habitat characteristics (mean \pm SD) of twelve salamander enclosures in interior forest, edge, and old-field habitats at the Baskett Wildlife Research Area, Boone County, Missouri.

	Forest	Edge	Field
pH	4.2 \pm 0.4	4.9 \pm 0.2	5.3 \pm 0.2
Cation exchange capacity (mequiv./100 g)	13.6 \pm 1.3	12.2 \pm 2.1	16.8 \pm 1.1
Organic matter (%)	2.7 \pm 0.2	2.9 \pm 0.6	3.6 \pm 0.7
Litter depth (cm)	3.9 \pm 0.4	3.3 \pm 0.3	1.4 \pm 0.1
Grass/herbaceous cover (%)	6 \pm 8	18 \pm 9	88 \pm 9
Canopy cover (%)	93 \pm 6	83 \pm 6	0
Eastern redcedar (<i>Juniperus virginiana</i> ; % composition)	1 \pm 1.2	24 \pm 11.0	—
Number of shrubs	10.8 \pm 12.8	33.0 \pm 33.1	1.0 \pm 1.4
Number of logs	1.8 \pm 1.5	0.8 \pm 1.5	0
Number of burrows (per 9 m ²)	3.5 \pm 1.9	1.8 \pm 1.2	1.9 \pm 1.2

the lowest percent organic matter (Table 2). On average, field soils had the highest cation exchange capacity (Table 2), which tends to be higher in soils with higher clay content (J.A. Stecker, personal communication (2002)). Field enclosures were characterized by dense herbaceous vegetation, and edge enclosures had higher shrub and herbaceous cover than forest enclosures (Table 2). In addition, eastern redcedars (*Juniperus virginiana* L.) comprised a larger proportion of the overstory at edge enclosures. Mean litter depth was highest in interior forest and lowest in fields, and we found more potential burrows (i.e., openings in the soil that, upon excavation, were found to be >8 cm long and >2 cm wide) in forest enclosures at the end of the study (Table 2).

Discussion

Using terrestrial enclosures, we tested the effects of habitat alteration and species on important demographic traits of pond-breeding amphibians. Our results indicate that the first few months in the terrestrial environment is the most critical period in determining survival rates of salamanders between metamorphosis and first reproduction. Even in edge and forest enclosures, the mean proportion known alive in the first

fall was only 38.5% for marbled salamanders and 16.7% for spotted salamanders. Similarly, Trenham et al. (2000) estimated that juvenile tiger salamanders experienced at least 50% mortality in the first few months post metamorphosis, which they attributed to harsh weather conditions (e.g., high temperature, low rainfall). By the second fall, mean proportion known alive in our study had declined to 28.1% for marbled salamanders and 13.5% for spotted salamanders. Survival to first reproduction of marbled salamanders in the study by Pechmann (1995) was 9% for males and 4% for females. In Scott’s (1994) study, 3%–15% of male and 3%–9% of female marbled salamanders returned to breed, depending on their larval density. By comparison, Semlitsch et al. (1988) estimated that 20% of mole salamanders from one cohort in South Carolina survived to first reproduction. However, mole salamanders have a shorter juvenile stage than either marbled or spotted salamanders.

One reason our estimates of survival are relatively high is that we terminated the study after only 2 years, whereas Pechmann (1995) continued his study for 6 years, until all salamanders had reached maturity. The flatness of our survivorship curves by fall of 2002, however, suggests that survival remained relatively constant in the latter part of the juvenile stage. Our populations also did not suffer predation-related

mortality, because most non-avian predators of amphibians were excluded; only two small snakes (genera *Carphophis* Gervais, 1843 and *Virginia* Baird and Girard, 1853) and six shrews were captured and removed from the enclosures during the 2 years of the study. On the other hand, some animals counted as dead may have actually escaped from our enclosures. Although we documented a few instances of salamanders trespassing over (or under) the dividing wall within an enclosure, we could not quantify rates of trespass over the exterior walls. It is safe to assume, however, that those rates were similar between species and habitats. Trespassing and the inability to distinguish permanent emigration from death are common problems in enclosure studies with amphibians (e.g., Pechmann 1995; Altwegg 2003). Such biases must be considered when interpreting survival estimates obtained from enclosures.

Juvenile survival in different habitats

As expected, old-fields were poor-quality habitats for juveniles of these species. Proportion known alive in field enclosures in the first fall was only 4.2% for marbled salamanders and 2.1% for spotted salamanders and dropped to zero for both species by the second fall. Owing to the susceptibility of amphibians to desiccation and heat stress, microclimatic factors such as soil moisture, temperature, and pH are important factors affecting the distribution of salamanders in the terrestrial environment (Spotila 1972; Wyman 1988; Parmelee 1993). Differences in abiotic factors like maximum temperature in summer and soil texture probably contributed greatly to the observed difference in survival between enclosures in fields and in forested habitats. Daily maximum temperatures in summer were much higher in fields than in either edge or forest and exceeded known critical thermal maxima. Clearly, tree canopy cover played an important role in maintaining suitable microclimatic conditions for the species we studied. Interestingly, Chazal and Niewiarowski (1998) found no significant differences in growth or survival of juvenile mole salamanders between pine forest and adjacent clearcuts in South Carolina, perhaps because temperature and soil moisture did not differ significantly between their habitat treatments.

Soil moisture was not a limiting factor in fields, because soil moisture in fields in the summer was intermediate between edge and forest enclosures, and forest soils tended to be the driest (Table 1). This observation is consistent with Chazal and Niewiarowski's (1998) finding that soils in clearcuts had higher water content than those in intact forest. This is most likely a result of higher evapotranspiration rates in forest, combined with the possible effects of past cultivation on soil permeability. In field enclosures, the clayey soils were typically saturated and poorly drained during the spring, then became hard and cracked as they dried in mid-summer. In contrast, water did not pool in forest enclosures and soils were looser in texture, which could have facilitated burrowing by salamanders. Spotted and marbled salamanders have limited burrowing ability (Semlitsch 1983) and rely instead on enlarging existing crevices or using rodent burrows (Douglas and Monroe 1981; Parmelee 1993; Loredó et al. 1996; Madison 1997). In general, climatic effects are mediated by the availability of burrows, which provide

cool, moist refuges (Seebacher and Alford 2002; Rothermel and Luhring 2005).

Although the effects of forest removal can extend some distance inside the physical forest edge (Yahner 1988; Murcia 1995), we found no evidence of negative edge effects on survival rates of ambystomatid salamanders. Our ability to detect edge effects was low, however. Despite placement of all edge enclosures on west-facing edges, there were substantial differences in microclimate and vegetation characteristics. Such within-treatment variability made it unlikely that we would see among-treatment differences given the low number of replicates. Among forest enclosures, survival varied greatly, yet there were no consistent patterns in habitat characteristics that correlated with survival. For example, survival and growth rates of both marbled and spotted salamanders were relatively low in one interior forest enclosure that had the highest litter depth and 100% canopy closure. There were no obvious differences in soil chemistry between this and other forest enclosures, thus the responses we observed must have been due to factors that we did not measure.

Differences in survival between species

Despite their larger size at metamorphosis (Fig. 2), spotted salamanders had slightly lower survival than marbled salamanders, which was likely due to the difference in timing of metamorphosis. Because they metamorphosed later, juvenile spotted salamanders were released under drier and warmer conditions than those experienced 1 month earlier by marbled salamanders. Under natural conditions, recently metamorphosed salamanders wait for rain to emigrate, but this strategy is not always effective. Shoop (1974) noted that several recently metamorphosed spotted salamanders apparently died of desiccation in leaf litter at the edge of a pond because it did not rain. Pough and Wilson (1970) found aggregations of juvenile spotted salamanders under rocks at the edge of a pond and noted that many of them showed signs of heat stress.

These observations elucidate another potentially significant advantage of metamorphosing early, in that marbled salamanders may enter a more benign terrestrial environment and may have more time to locate refuges before the weather becomes hot and dry. After the onset of hot weather, juveniles probably have limited opportunities to feed and may be forced to rely on energy reserves, pointing to another advantage of larger mass at metamorphosis (Scott 1994). Thus, in addition to providing larvae with a competitive advantage in the aquatic environment, fall breeding may improve chances of survival early in the terrestrial stage. Differences in timing of metamorphosis have previously been demonstrated to be important determinants of age and size at maturity within species (Smith 1987; Semlitsch et al. 1988). Specifically, mole salamander larvae that metamorphosed early attained a larger size at first reproduction, which was attributed to juveniles having better conditions or simply more time for foraging in the terrestrial environment (Semlitsch et al. 1988).

Carry-over effect of size at metamorphosis on survival

Juveniles that were larger in terms of mass had better chances of surviving the first few months in the terrestrial

environment. Larger body mass could improve chances of survival because the rate of evaporative water loss decreases with increasing surface area to volume ratio (Spight 1968; Spotila 1972). Other proposed mechanisms for a size advantage in juveniles are reduced chances of predation (Berven 1990) and reduced risk of parasitic infection (Goater 1994). Pechmann (1994) found that metamorphosing at a smaller size decreased survival to first reproduction of male mole salamanders. Likewise, Scott (1994) found that 21% of marbled salamanders raised at low larval densities (thus larger in size) returned to breed, compared with 6% of marbled salamanders raised at high densities. Other studies have found no relationship between size at metamorphosis and survival to first reproduction (Smith 1987; Semlitsch et al. 1988). The potential effects of body size on dispersal tendency in amphibians are still unknown (Scott 1994). However, sites with high larval density and poor-quality terrestrial habitat would be expected to produce fewer successful dispersers.

Habitat and density effects on juvenile growth and time to maturity

Proximity to forest edges did not affect growth rates of surviving individuals. Thus, we found no evidence that proximity to forest edges incurs fitness costs for ambystomatid salamanders in terms of smaller size or later age at maturity. We also did not detect an effect of density on mass or length of juvenile salamanders that survived past the first summer, indicating that the maximum density of surviving individuals in our enclosures (0.67 per m² for marbled salamanders, 0.44 per m² for spotted salamanders) was not high enough to induce negative density-dependent effects.

Pfingsten and Downs (1989) reported an adult minimum size of 45 mm for marbled salamanders in Ohio, and Scott (1994) reported a minimum size of 48–49 mm for females in his South Carolina population. Some of the juvenile marbled salamanders in our study attained these sizes by their first fall following metamorphosis. The sizes of the mature male spotted salamanders that we captured in fall of 2002 (65–77 mm SVL) were within the range reported by Sexton et al. (1986) for mature males in a population in eastern Missouri (60–89 mm SVL). The smallest mature spotted salamanders in a Massachusetts population were 56.5 mm SVL and 5.0 g for males and 60.2 mm and 7.0 g for females (Windmiller 1996). Windmiller (1996) found that some male spotted salamanders at his study site in Massachusetts attained sexual maturity during the 2nd year following metamorphosis, whereas females took an additional year. Similarly, in our study, spotted salamanders grew more slowly than marbled salamanders in the 1st year and did not reach minimum adult size until the second fall following metamorphosis. Only males reached maturity in the 2nd year, even though all females exceeded 67 mm SVL by the fall of 2003 (range 67–79 mm SVL).

In conclusion, nearly all previous studies of the effects of forest removal on amphibian populations have used relative abundance to measure the response of amphibians to habitat disturbance (deMaynadier and Hunter 1995). It is impossible to discern from abundance data the underlying factors responsible for differences; for example, is the relatively low abundance in altered habitats such as clearcuts a function of

behavioral avoidance, lower survival in these habitats, or both? Gibbs (1998b) noted that both spotted salamanders and marbled salamanders will cross forest edges to access breeding pools in open habitats, but little is known regarding movement behavior of juveniles. Rothermel and Semlitsch (2002) found that most juvenile spotted salamanders avoided fields during their initial emigration from pools on forest-field edges. Sixteen percent of emigrating spotted salamanders and 18% of small-mouthed salamanders oriented toward fields initially, with some later reversing direction and returning to the pools. In another study (Rothermel 2004), from 1 to 79 days elapsed between releases of postmetamorphic spotted salamanders in pastures and their recapture at forest edges up to 50 m away. In all, 20% of the salamanders that were recaptured at the forest edge survived at least 2 weeks in the pastures (B.B. Rothermel, unpublished data). Thus, the question remained, what is the fate of individuals that do not avoid relatively inhospitable habitats?

Taken together, results of this and previous studies suggest old fields and other open habitats are not absolute barriers to movement by juvenile salamanders. Juveniles that do not exhibit behavioral avoidance of such habitats, however, have very low probabilities of survival. The degree to which these habitats affect movement rates between patches of forest is a function of distance and time spent traversing the matrix habitat, as well as the timing of metamorphosis and migration with respect to environmental conditions. Because many pond-breeding amphibians exhibit metapopulation or source-sink dynamics, dispersal is essential for recolonization of extinct local populations and persistence of species at the landscape scale (Gill 1978; Sinsch 1992; Sjogren-Gulve 1994; Semlitsch 2000; Marsh and Trenham 2001). In addition, population growth rates of ambystomatids are sensitive to postmetamorphic survival (Biek et al. 2002; Vonesh and de la Cruz 2002). Thus, breeding sites with a high proportion of non-forested habitat in the surrounding landscape may be sinks because of high mortality of juveniles in the first few months post metamorphosis. Our results lend additional support to recommendations to preserve forested buffers around amphibian breeding sites (Semlitsch 1998). Additional research is needed, however, to determine whether ambystomatids are negatively affected by the increase in edge habitat that accompanies forest fragmentation.

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