CRITICAL THRESHOLDS ASSOCIATED WITH HABITAT LOSS FOR TWO VERNAL POOL-BREEDING AMPHIBIANS

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Abstract. A critical threshold exists when the relationship between the amount of suitable habitat and population density or probability of occurrence exhibits a sudden, disproportionate decline as habitat is lost. Critical thresholds are predicted by a variety of modeling approaches, but empirical support has been limited or lacking. We looked for critical thresholds in two pool-breeding amphibians that spend most of the year in adjacent upland forest: the spotted salamander (Ambystoma maculatum) and the wood frog (Rana sylvatica). These species were selected because of their reported poor dispersal capacities and their dependency on forest habitat when not breeding. Using piecewise regression and binomial change-point tests, we looked for a relationship between the probability of occupancy of a site and forest cover at five spatial scales, measuring forest cover in radial distances from the pond edge of suitable breeding ponds: 30 m, 100 m, 300 m, 500 m, and 1000 m. Using piecewise regression, we identified significant thresholds for spotted salamanders at the 100-m and 300-m spatial scale, and for wood frogs at the 300-m scale. However, binomial change-point tests identified thresholds at all spatial scales for both species, with the location of the threshold (percent habitat cover required) increasing with spatial scale for spotted salamanders and decreasing with spatial scale for wood frogs. Thresholds for spotted salamanders occurred at $\sim 30\%$ forest cover at spatial scales of 100 m or less, with 41% cover at 500 m, and with 51% habitat cover at 1000 m. Thresholds for wood frogs ranged from 88% habitat cover at 30 m from the pond edge, declining to 44% habitat cover within 1000 m. These patterns might be explained by the different winter dispersions of these species. Knowing whether a species has a critical threshold, and at what level of cover and at what spatial scale it exists, would be essential for conservation of habitat-sensitive species.

Key words: Ambystoma maculatum; amphibian; conservation; extinction threshold; forest cover; habitat; Rana sylvatica; spatial scale; spotted salamander; vernal pool; wood frog.

INTRODUCTION

Habitat loss and fragmentation are the most influential mechanisms increasing species extinction risk (Ehrlich 1988, Kareiva and Wennergren 1995, Wilcove et al. 1998). Increased risk is due to decreased population size, increased isolation, and edge effects. As habitat is lost, there is some minimum patch size necessary for a species to occupy an isolated patch on a landscape (e.g., Robbins et al. 1989, Askins 1994). A developing hypothesis in landscape and conservation biology is the existence of threshold levels of habitat loss and fragmentation that result in a sudden reduction in occupancy despite the presence of sufficient suitable habitat (Gardner et al. 1987, Andrén 1994, With and Crist 1995, Fahrig 2001). Models based on percolation theory suggest that as the percentage of habitat lost increases, patch size decreases and isolation increases

in a nonlinear fashion (e.g., Keitt et al. 1997). Thus, the relationship between habitat loss and population density also might be nonlinear. These critical thresholds are predicted from several modeling approaches (e.g., Lande 1987, With and King 1999, Keymer et al. 2000, Fahrig 2001), but empirical support is limited or lacking. This ambiguity exists, in part, because few field studies are designed specifically to look for thresholds (Andrén 1994, Gibbs 1998*a*), and we are aware of no studies looking for species-specific thresholds at multiple spatial scales. If such thresholds exist, identifying them is essential for understanding population dynamics and extinction processes, and would be important to landscape management and reserve design.

There is disagreement over how much habitat loss should be associated with a threshold. Early percolation modeling predicted a threshold at 59% cover, finding that these landscapes were qualitatively less connected. This value is now recognized as an artifact of using lattice percolation, which only allows for "north– south" and "east–west" movement on a landscape. A more general model, bond percolation, still results in thresholds in connectivity, so-called percolation transitions, but the threshold is dependent on dispersal abil-

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ity (Keitt et al. 1997). This result is supported when a fractal, rather than random, distribution of patches is used, resulting in thresholds at 29–50% cover, depending on habitat arrangement (With et al. 1997, Hill and Caswell 1999, Fahrig 2002).

Empirical support of critical threshold relationships between habitat cover and patch occupancy or population density is debated. For example, Andrén (1994) reviewed bird and mammal literature and reported evidence of thresholds in occupancy at levels of habitat cover of 10–30%. However, Mönkkönen and Reunanen (1999) reviewed the same studies and concluded that evidence was lacking (see Andrén [1999] for a response). The majority of threshold studies of natural populations have focused on birds and small mammals (e.g., Andrén 1994, Carlson 2000), and we know of only one study on amphibians (Gibbs 1998*a*).

Globally, scientists and citizens are concerned about declines of amphibians, a group of organisms that play important roles in ecosystem function (Seale 1980) and that may act as indicators of environmental problems (Blaustein and Wake 1995, Homan et al. 2003). Although habitat loss is likely to be the primary cause of many of these declines (Wyman 1990, Blaustein et al. 1994, Pounds et al. 1999), the relationship between the amount of habitat lost and the degree of amphibian decline is unknown. Differing dispersal abilities and often highly fluctuating population sizes can complicate this relationship, leading to the prediction (cf. Gardner et al. 1987, Gibbs 1998a, Fahrig 2001) that some amphibians should be more prone to critical thresholds. In a study of forest-dwelling amphibians along an urban to rural gradient in New England, Gibbs (1998a) found thresholds in occupancy in three of the five species that he examined, but the thresholds did not occur at a consistent level of forest cover between species, and only a single spatial scale was investigated.

We investigated whether two pond-breeding amphibians, spotted salamanders (Ambystoma maculatum) and wood frogs (Rana sylvatica), exhibit thresholds in their probability of occupancy as surrounding forest habitat is lost. These species breed in vernal pools and spend the rest of the year (up to 50 weeks) in forest habitat near the pools. Because of differences in dispersal and winter dispersion patterns between these species, and because of a relative lack of information on the spatial scale at which these species use the landscape, we looked for thresholds at multiple spatial scales. Although both species occupy forest habitat within 300 m of the pond edge (Windmiller 1996; Regosin et al., in press), adult wood frogs have a greater dependence on forested wetland for summer activity (DeGraaf et al. 1983), and they remain closer to the pond in winter (Regosin et al., in press). However, wood frogs appear to have greater dispersal distances than do spotted salamanders (Kleeberger and Werner 1983, Madison 1997, Semlitsch 1998; but see Gordon 1968). Berven and Grudzien (1990) have estimated wood frog genetic neighborhoods to be 1.0-1.2 km in size, whereas adult spotted salamanders seem to have maximum dispersal distances near 0.25 km per year. Consequently, we predicted that these two species might respond at different spatial scales to habitat loss, with wood frogs being impacted at a larger spatial scale than spotted salamanders.

Methods

Study organisms

Potential breeding sites in eastern Massachusetts (USA) were surveyed for two amphibian species, spotted salamanders and wood frogs. We selected sites in a relatively uniform suburban habitat to avoid complications associated with changes in an urban to rural gradient (e.g., Gibbs 1998a). These amphibians are widely distributed throughout eastern North America. Both species spend most of the year foraging and overwintering in wooded areas surrounding small vernal or semi-permanent water bodies (Downs 1989, Windmiller 1996; Regosin et al., in press). In our study area, spotted salamanders and wood frogs generally migrate to the breeding pond between February and April. Spotted salamanders spend between a few days and three weeks in the breeding pond (Shoop 1968), after which they return to the upland for the remainder of the year, where they tend to use hilly, well-drained soils (Windmiller 1996).

Data collection

Field surveys were conducted during the springs of 1993 and 1994 in Concord, Massachusetts (42°27' N, 71°21' W), a suburb \sim 30 km northwest of Boston, Massachussetts. In total, 168 ponds were identified by previous inventory work (Windmiller 1990) or through random selection of ponds visible on color infrared aerial photographs of the area. A combination of aerial photograph examination and field searches suggests that 60-70% of potential breeding sites were surveyed (Windmiller 1996). For each pond, one of us (B.S. Windmiller) determined presence or absence of spotted salamanders and wood frogs by walking through the basins of the ponds and counting egg masses (Windmiller 1996) or by dip-netting for larvae when pond surveys were conducted late enough in the season that eggs might have already hatched. Slightly fewer ponds (165) were searched for evidence of wood frog presence, because wood frog egg masses hatched more rapidly than spotted salamander egg masses. Compass-line transects were used in large ponds to increase the chance of encountering egg masses (Windmiller 1996).

Using aerial photographs taken in 1991, land cover variables were measured for five radial distances: 30 m, 100 m, 300 m, 500 m, and 1000 m from the pond edge. Upland habitat was characterized as one of four types (developed, flooded, wetland forest, or upland

forest), as indicators of available habitat types. Developed habitat was characterized by buildings, lawns, roads, and agricultural fields with <50% tree cover; flooded habitat was characterized by tree-less water bodies that are either permanent or meet the criteria for a potential breeding pond for spotted salamanders or wood frogs; wetland forest consisted of areas with >50% tree cover and saturated soils with possible seasonal flooding; upland forest was characterized as an area with >50% tree cover and well-drained soils (Windmiller 1996). The percentages of each habitat type included within each of the five concentric zones were calculated using a standard dot grid.

Analyses

We considered suitable habitat for spotted salamanders to be upland forest (Windmiller 1996); for wood frogs it was upland forest and wetland forest (DeGraaf et al. 1983; Regosin et al., in press). Two statistical methods were used to look for thresholds. For the first analysis, we divided percent habitat cover into 10% intervals (deciles) and calculated the percentage of ponds occupied in each decile. Potential thresholds in percentage occurrence initially were identified visually from the plots for all possible spatial scales for each species based on a dramatic change in the relationship between these variables. We then tested for significance of visually identified potential thresholds with piecewise regression weighted by the number of ponds in each decile (Neter et al. 1996, Toms and Lesperance 2003). We also systematically evaluated our informal threshold cover determinations using weighted piecewise regressions considering each decile as a potential break point (threshold); statistical analyses were done using SAS version 8.2 (SAS Institute 1999).

We also used a nonparametric binomial change-point test (Siegel and Castellan 1988), which evaluates a series of presence–absence data relative to habitat cover and finds the habitat cover value at which the difference in 1's vs. 0's is maximized. The statistical test determines whether or not the proportion of 1's is significantly different above vs. below the change point. Raw, rather than decile, data were used.

We did not adjust P values within each set of multiple tests, because we agree with Moran (2003) that, for exploratory studies, it can be valuable to avoid relegating potentially important results to insignificant status when there is not enough statistical power to support post hoc adjustments. Consequently, these analyses should be treated as exploratory.

RESULTS

Our visual analysis identified potential thresholds in occurrence for spotted salamanders at 100 m and 300 m from the pond edge, at $\sim 20-30\%$ forest cover (Fig. 1b, c). No thresholds were apparent at the 30, 500, and 1000 m radii (Fig. 1a, d, e). Statistical evidence from the piecewise regression suggests that there were sig-

nificant thresholds in spotted salamander occurrence at both the 100 m and 300 m distances (F = 6.23, df = 2, 7, P = 0.041 and F = 6.91, df = 2, 7, P = 0.034, respectively). For wood frogs, our visual analysis suggested possible thresholds at 100 m and 300 m from the pond edge (Fig. 2b, c). These apparent thresholds fell at 20–30% forest cover for the 100 m radius and at 10–20% forest for the 300 m radius. However, only the threshold at 300 m was statistically significant (F= 5.63, df = 2, 7, P = 0.049).

For most cases, the sliding piecewise regressions confirmed the visually selected location of the significant thresholds that we initially identified, both for spotted salamanders and for wood frogs. However, for spotted salamanders at the 100 m radius, we statistically identified three additional cover values at which statistically significant thresholds existed: 30-40%, 40-50%, and 50-60% (F = 7.15, df = 2, 7, P = 0.032; F = 8.02, df = 2, 7, P = 0.025; and F = 6.80, df = 2, 7, P = 0.035, respectively). We did not find statistically significant thresholds for either species at any other spatial scales (all P > 0.05).

Results obtained from the nonparametric binomial change-point tests showed that significant thresholds were present at all spatial scales for both species, but that the location of the thresholds differed across spatial scales for each species (P < 0.01 for all; Table 1). For spotted salamanders, thresholds existed at approximately the same percent habitat cover at 30, 100, and 300 m from the pond edge (32%, 28%, and 34%, respectively). However, percent habitat cover requirements appeared to increase at the larger spatial scales of 500 and 1000 m (41% and 51%, respectively). For wood frogs, the threshold at the greatest percent habitat cover value (88%) was at the smallest spatial scale, 30 m, with a systematic decline in threshold cover as distance from the pond increased; at 1000 m, the threshold fell at 44% habitat cover.

DISCUSSION

We discovered critical thresholds for both spotted salamanders and wood frogs, and these thresholds changed with spatial scale. Using piecewise regression, we found that spotted salamanders showed apparent thresholds in occupancy when forest cover was considered within 100 m and 300 m from the edge of the breeding pond, but not at smaller (30 m) or greater (500 m, 1000 m) spatial scales. Thresholds in wood frog occupancy occurred only when forest cover was measured within 300 m of the pond edge. In most cases where significant thresholds were found, they fell between 10% and 30% cover, as predicted by Andrén (1994). These results are consistent with those of Gibbs (1998*a*), who found critical thresholds for both of these species at \sim 30% forest cover.

In contrast, the binomial change-point test identified thresholds for both species at all spatial scales. These results suggest that the binomial change-point test may



FIG. 1. Percentage occurrence of spotted salamanders (*Ambystoma maculatum*) vs. percentage of upland forest at five different spatial scales, measured from the edge of suitable breeding ponds. Straight lines were determined by linear regressions weighted by sample size in each decile. Where there is one line per graph, no significant threshold was identified, and this is the best-fit weighted linear regression. Where there are two regression lines, they show the location of a critical threshold. In panel (c), the lines represent the break identified a priori by visual inspection; there were three other statistically significant break points (see *Results* for details).

be a more sensitive indicator of thresholds for our data, possibly because all data points are used rather than using aggregated data (i.e., binned by decile). The critical thresholds varied by spatial scale and species. First, the analyses suggest that wood frogs are more sensitive to habitat loss near the pond than are spotted salamanders. This could be due to the relative importance of winter habitat. Regosin et al. (in press) found that wintering wood frogs are at highest density near the pond, and densities decline rapidly as distance from the pond increases. Wood frogs' disproportionate use of habitat closest to ponds might explain the high sensitivity to habitat loss at the 30 m radius (critical threshold at 88% habitat cover) and the 100 m radius (at 78% habitat cover). Spotted salamanders, on the other hand, are at a uniform low density at all distances within 300 m of the pond. This latter observation might explain the consistent habitat cover level associated with critical thresholds for spotted salamanders. We also found that spotted salamanders and wood frogs tended to converge in habitat covers associated with thresholds as distance from the pond increased. This means that with increase distance from the pond, spotted salamanders were more sensitive to habitat loss, whereas wood frogs were less sensitive. This pattern was the opposite of what we predicted based on the greater dispersal distances of wood frogs relative to spotted salamanders (DeGraaf et al. 1983, Kleeberger and Werner 1983, Berven and Grudzien 1990, Madison 1997, Semlitsch 1998).

Mönkkönen and Reunanen (1999) and Fahrig (2001) predicted that the location and slope of a critical threshold should be species specific, based on a variety of traits, including reproductive potential, emigration success, territory size, habitat specificity, dispersal ability, and other behaviors (see also Andrén et al. 1997, Bender et al. 1998). Recent models predict thresholds at 29–



FIG. 2. Percentage occurrence of wood frogs (*Rana sylvatica*) vs. percentage of upland and wetland forest remaining at five different radial distances from the edge of suitable breeding ponds. Straight lines represent weighted linear regressions. Where there is one line per graph, no significant threshold was identified. Where there are two regression lines, they show the location of a significant extinction threshold.

50% cover, depending on habitat arrangement (With et al. 1997, Hill and Caswell 1999, Fahrig 2002), and Andrén (1994) and Gibbs (1998*a*) have observed thresholds at the lower end of this range. These predictions are similar to what we observed for spotted salamanders at all spatial scales, and for wood frogs at larger spatial scales. A critical threshold at the upper range of model predictions also was observed for Baybreasted Warblers (*Dendroica castanea*), which have been found to be absent from landscapes with <55% forest cover (Drolet et al. 1999). The critical threshold that we observed for wood frogs at smaller spatial scales at such high cover values was not predicted by current threshold models.

Habitat loss often results in increased fragmentation, and both loss and fragmentation may contribute to the occurrence and location of thresholds (Keitt et al. 1997). For example, if habitat loss results in a smaller, but unfragmented forest, the threshold of occurrence

may be different than if habitat loss results in many small, fragmented forest patches. Although we did not measure fragmentation, it is possible that fragmentation was at least partially responsible for the thresholds that we observed (Gibbs 1998a). Both wood frogs and spotted salamanders demonstrate high site fidelity to their breeding pond and, in some cases, to their upland habitat (Husting 1965, Williams 1973, Berven and Grudzien 1990). This site fidelity might inhibit animals from switching from a breeding pond with reduced suitable habitat to one with more suitable habitat. Also, although individuals of both species can disperse >200m from their breeding ponds (Berven and Grudzien 1990, Windmiller 1996), and might attempt to disperse, they may be poorly equipped to disperse through typical suburban matrix. Most of the suburban matrix in our study area was unforested lands used for agriculture, housing developments, or industry, and several studies have shown that both spotted salamanders and

TABLE 1. Location of critical threshold (percent cover) based on a nonparametric binomial change-point test at five radial distances from the pond edge, for spotted salamanders and wood frogs.

			No. ponds		
Distance from pond edge	Critical threshold (% cover)	$D_{\scriptscriptstyle m,n}$ †	Occu- pied (m)	Unoccu- pied (n)	Р
Spotted salamander					
30 m	32	0.378	80	88	< 0.001
100 m	28	0.478	79	89	< 0.001
300 m	34	0.408	79	89	< 0.001
500 m	41	0.427	75	83	< 0.001
1000 m	51	0.404	75	83	< 0.001
Wood frog					
30 m	88	0.289	85	72	< 0.01
100 m	78	0.305	85	72	< 0.01
300 m	55	0.355	85	72	< 0.001
500 m	55	0.327	85	70	< 0.001
1000 m	44	0.396	85	70	< 0.001

[†] The test statistic for the nonparametric binomial changepoint test.

wood frogs avoid crossing fields, pastures, clearcuts, lawns, and wide roads (Windmiller 1996, Gibbs 1998*b*, and deMaynadier and Hunter 1999, Rothermel and Semlitsch 2002; Regosin et al., *in press*), thus limiting their ability to disperse to nearby suitable habitat patches.

Our study demonstrates the importance of considering spatial scale when looking for critical thresholds, either theoretically or empirically (Keitt et al. 1997). Examination of multiple spatial scales provides information about the spatial scale at which species persistence is affected by habitat quantity, which is crucial to conservation management decisions. As an example from our study region, the Massachusetts Wetlands Protection Act (Massachusetts General Laws, Chapter 131, section 40) allows for protection of terrestrial habitat up to 30 m surrounding amphibian breeding sites. Based on our results, spotted salamanders and wood frogs are clearly affected by habitat loss at much greater distances from the pond edge. Similar criticisms of upland regulatory practices also have been made by others (Semlitsch 1998, Semlitsch and Bodie 1998, 2003).

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