hábitat terrestre de buena calidad alrededor de los humedales con la declinación y riesgo de extinción de poblaciones locales de anfibios. Estas simulaciones mostraron que las regulaciones estatales actuales que protegen 30 m o menos del hábitat terrestre circundante son inadecuadas para soportar poblaciones viables de anfibios que se reproducen en charcas. También encontramos que las especies con estrategias de historia de vida diferentes respondieron de manera distinta a la pérdida y degradación del hábitat terrestre. R. sylvatica, *con un ciclo de vida corto y alta fecundidad, fue más sensible a la pérdida de hábitat y aislamiento, mientras que* A. maculatum, *más longeva y con menor fecundidad, fue más sensible a la degradación del hábitat que redujo las tasas de supervivencia de adultos. Los resultados de nuestro modelo demuestran que una alta probabilidad de persistencia de una población local de anfibios requiere de suficiente hábitat terrestre, del mantenimiento de la calidad del hábitat y de la conectividad entre poblaciones locales. Nuestros resultados enfatizan el papel esencial del hábitat terrestre adecuado para el mantenimiento de la biodiversidad de humedales y el funcionamiento del ecosistema y ofrecen un medio para cuantificar los riesgos asociados con la pérdida y degradación del hábitat terrestre.*

Palabras Clave: *Ambystoma maculatum*, conservación de humedales, demografía de anfibios, humedal aislado, modelo matricial, *Rana sylvatica*, viabilidad poblacional,

Introduction

Terrestrial habitat adjacent to wetlands is essential to the maintenance of wetland biodiversity (Findlay & Houlahan 1997; Calhoun & Klemens 2002) and thus to the integrity of wetland ecosystems. Alteration of this terrestrial habitat by human land-use can cause declines and local extinctions of wetland-dependent organisms (Findlay & Houlahan 1997). Population declines can occur owing to direct mortality from human activities (e.g., road mortality or clearing of wetland plants) or indirectly as a result of habitat loss and degradation, which may lower carrying capacity and reduce annual survival rates (Gibbs 1998). Local extinctions may also occur when land-use isolates small populations, preventing immigration and recolonization (Gibbs 2000). Taxa with limited dispersal ability, including amphibians, reptiles, and small mammals, are especially susceptible to local extinction when habitat loss and degradation around wetlands impede movement among local populations (Findlay & Houlahan 1997).

Although the Clean Water Act regulates the draining and filling of wetlands in the United States, federal regulations do not protect most isolated wetlands or extend protection to surrounding terrestrial habitat. Some land managers, city planners, and policy makers at the state and local levels are making an effort to protect such wetlands and their associated biodiversity (Calhoun et al. 2005). For example, Massachusetts protects a terrestrial "buffer zone" of 30 m around some isolated wetlands. This buffer area protects wetlands somewhat, but does not provide adequate terrestrial habitat to maintain populations of many wetland-dependent birds, mammals, amphibians, reptiles, and plants (Findlay & Houlahan 1997; Semlitsch & Bodie 2003; Gamble et al. 2006). Buffer zones intended to protect aquatic habitats do not adequately protect the quality of adjacent terrestrial habitat, which must also be buffered from surrounding land-use practices if wetland biodiversity is to be maintained (Semlitsch & Jensen 2001). Striking a feasible balance between human land use and habitat conservation is challenging, and the specific risks associated with varying amounts of terrestrial habitat loss and degradation are often difficult to quantify, complicating the progress of well-informed land-use policy.

Habitat loss is implicated in the decline of many amphibian species currently threatened with global extinction. Amphibians that breed in wetlands in temperate forests require aquatic breeding habitat and terrestrial summer foraging and overwintering habitat to maintain viable populations (Regosin et al. 2003*a*, 2003*b*). An analysis of data from the literature on 32 amphibian species suggests that core terrestrial habitat (the area encompassing 95% of the adults in a population) extends on average 159–290 m from the breeding site (Semlitsch & Bodie 2003). Results of several other studies show that adult amphibians regularly use terrestrial habitat as far away as 1 km or more from the breeding site (reviewed in Patrick et al. 2006). 1 Km = 3280 ft.

Recent demographic models of amphibian population dynamics demonstrate that population growth in several species is extremely sensitive to changes in terrestrial juvenile and adult survival rates (Biek et al. 2002; Vonesh & De la Cruz 2002). In addition, numerous landscape-scale studies correlate the amount of forest cover within the core terrestrial habitat area with the presence or absence of many amphibian species (e.g., Homan et al. 2004; Rubbo & Kiesecker 2005), which suggests that even when aquatic habitat is maintained, degradation and loss of terrestrial habitat can lead to amphibian declines and extinctions.

To evaluate the population-level consequences of reductions in terrestrial habitat for pool-breeding amphibians, we used published demographic data to develop matrix population models for 2 amphibian species, the wood frog (*Rana sylvatica*) and spotted salamander (*Ambystoma maculatum*). Both species depend on forest and breed in isolated wetlands throughout the northeastern United States. Nevertheless, differences in their life-history strategies and population dynamics may result in differing responses to terrestrial habitat loss.

Through model simulations, we predicted the decline and risk of extinction of wood frog and spotted salamander populations resulting from truncation of terrestrial habitat surrounding wetland breeding sites. Using an approach similar to that taken by Trenham and Shaffer (2005), we ran simulations for both species to estimate population size and probability of persistence resulting from a range of terrestrial habitat areas. We also evaluated how these predictions are influenced by reductions in habitat quality within the remaining terrestrial habitat and by the degree of connectivity among local populations.

Methods

Study Species

Wood frogs and spotted salamanders are explosive breeders, migrating from terrestrial overwintering habitat in upland areas to wetland breeding sites in early spring. Although the 2 species have similar habitat requirements, they differ markedly in other aspects of their life-history strategies. Clutch sizes of wood frogs often contain over a thousand eggs (Berven 1988), whereas female spotted salamanders oviposit approximately 100–300 eggs (Shoop 1974). Wood frogs are short-lived, and most individuals breed only once or twice in a lifetime (Berven 1990), whereas some spotted salamanders may live as long as 32 years (Flageole & Leclair 1992) and can breed annually after reaching reproductive maturity. Female spotted salamanders may occasionally skip a year of breeding, possibly due to weather conditions or resource availability (Blackwell et al. 2004). Wood frog females can mature in as little as 1 year, but may take up to 4 years in some populations (Bellis 1961; Berven 1990, 1995). Female spotted salamanders, in contrast, do not typically reach reproductive maturity until 3–5 years of age and can take as long as 7 years (Wilbur 1977; Flageole & Leclair 1992).

In pool-breeding amphibian populations successful metamorphosis largely depends on breeding-site hydroperiod (Pechmann et al. 1991). Results of a study conducted in Rhode Island (U.S.A.) estimated that wood frogs and spotted salamanders require a hydroperiod of approximately 112–144 days and 155–211 days, respectively, for successful reproduction and metamorphosis. Catastrophic mortality occurs in years with low rainfall, when pools dry before animals reach metamorphosis, and high survival occurs in years with high rainfall (Pechmann et al. 1991). These boom and bust years lead to large fluctuations in the size of adult wood frog populations (Howard & Kluge 1985; Berven 1990, 1995). Fluctuations in adult spotted salamander populations are likely buffered by their longevity, which allows individuals from boom years to accumulate over time in the adult population (Husting 1965; Whitford & Vinegar 1966).

Model Structure and Parameterization

We developed stage-based stochastic matrix population models for the wood frog and spotted salamander. The wood frog model included 4 life-history stages: premetamorphosis (egg and larval stages) and 1, 2, and 3 years old. The salamander model had a similar structure, but terrestrial life-history stages were divided into juvenile and adult stages rather than age categories because age-based categories would be intractable due to salamander longevity. For both species the models tracked only females, which lay 1 clutch per year, whereas males can fertilize multiple clutches and are therefore not considered limiting to population growth. The models were post-breeding models, with simulations projecting the population on an annual basis from the end of one reproductive season to the next.

We parameterized the models with published species-specific demographic data (Tables 1 & 2). When possible, we based estimates on populations from the northeastern United States because demographic rates can vary geographically. We also used estimates specific to females if these data were available. For the wood frog model we used estimates of vital rates in Berven (1990) as part of a 7-year study of a wood frog population in Beltsville, Maryland (U.S.A.). We not only based estimates of spotted salamander vital rates on a 5-year study of spotted salamanders in Massachusetts (U.S.A.) (Shoop 1974) but we also included data from additional sources (Table 2). Multiple estimates of each parameter were used in the models, drawn randomly at specified frequencies during each year of the simulations (Tables 1 & 2).

We used functional relationships between spring rain and survival to metamorphosis to incorporate environmental stochasticity into the wood frog and spotted salamander models. For the wood frog model we used data from the Beltsville, Maryland, weather station (noaa.gov) to develop a functional relationship between spring rainfall and premetamorphic survival rates reported in Berven (1990) for the years 1976–1980 ($y = 0.003x - 0.062$, where y is premetamorphic survival and x is rainfall; $r^2 = 0.60$). We used this relationship and weather-station data from 1950 to 2005 (all available years) to estimate the range and frequencies of premetamorphic survival rates (Table 1). We used this same method for spotted salamanders. We used weather data from the East Milton Blue Hill Observatory (noaa.gov) to estimate the relationship between spring rainfall and the probabilities of survival to metamorphosis reported in Shoop (1974) for the years 1964–1968 ($y = 0.0008x - 0.0298$; $r^2 = 0.97$). We used this relationship and rainfall data from 1906 to 2005 (all available years) to predict premetamorphic survival rates

Table 1. Parameter estimates and frequencies at which each estimate was drawn during matrix model projections of wood frog populations.[a]

Parameter	*Estimates*	*Frequency*
Premetamorphic survival	0	0.058
	0.013	0.327
	0.033	0.308
	0.053	0.135
	0.073	0.115
	0.090	0.058
Survival from metamorphosis to 1 year	0.25	0.250
	0.38	0.500
	0.50	0.250
One-year-old survival to 2-year-old	0.14	0.150
	0.18	0.350
	0.21	0.350
	0.61	0.150
Two-year-old survival to 3-year-old	0.08	0.150
	0.09	0.350
	0.12	0.350
	0.23	0.150
Premetamorphic fecundity[b,c]	0	0.150
	0.02	0.350
	0.10	0.350
	0.26	0.150
Fecundity of 1-year-old[c,d]	40.88	0.150
	50.70	0.350
	71.50	0.350
	229.06	0.150
Fecundity of 2-year-old[c,d]	29.43	0.150
	30.08	0.350
	43.72	0.350
	68.80	0.150

[a] *Parameter estimates come from Berven (1990). These estimates and the frequencies at which they are drawn yield a stochastic log growth rate of 1 in model simulations assuming no immigration.*

[b] *Premetamorphic individuals have fecundity in this model because it is a postbreeding model in which the projection interval is 1 year and reflects the number of individuals in each life-history stage shortly after breeding has occurred. Some individuals that are premetamorphic (eggs) at 1 projection interval can hatch, metamorphose, and produce eggs of their own by the following breeding season. Thus, premetamorphic individuals can have fecundity, although their per capita fecundity values are low because most females do not mature within 1 year.*

[c] *In a postbreeding model, females must survive for 1 year to be able to reproduce before the following projection interval. Fecundity is equal to clutch size times annual survival times 50% (the model tracks only females in the population and assumes that 50% of each clutch is female).*

[d] *Fecundity of 2-year-olds is lower than the fecundity of 1-year-olds in this model not because of differences in clutch sizes, but because 2-year-olds have lower survival.*

Table 2. Parameter estimates and frequencies at which each estimate was drawn during projections of spotted salamander populations.*

Parameter (reference)	*Estimate*	*Frequency*
Premetamorphic survival (Shoop 1974)	0	0.05
	0.025	0.10
	0.045	0.29
	0.065	0.26
	0.085	0.15
	0.125	0.07
	0.150	0.08
Survival from metamorphosis to juvenile (Rothermel & Semlitsch 2006)	0	0.37
	0.08	0.13
	0.17	0.37
	0.25	0.13
Juvenile survival	0.76	1
Adult survival (Whitford & Vinegar 1966; Husting 1965)	0.7	0.33
	0.8	0.34
	0.9	0.33
Transition from juvenile to adult (Wilbur 1977)	0.33	0.33
	0.25	0.34
	0.20	0.33
Clutch size (Shoop 1974)	224	1
Breeding frequency (Whitford & Vinegar 1966; Blackwell et al. 2004)	0.75	0.25
	0.89	0.50
	0.90	0.25

**Parameter estimates were based on published data with the exception of juvenile survival that was set at 0.76, a value that yielded a stochastic log growth rate of 1 after all other model parameters had been estimated in simulations assuming no immigration.*

and frequencies (Table 2). On the basis of these relationships, catastrophic years in which survival to metamorphosis is zero occurred in 5.8% of years for wood frogs and in 5% of years for spotted salamanders.

We assumed that 1- and 2-year-old wood frog survival was highly correlated within years because both age classes experience the same environmental conditions and adult survival is highly correlated with rainfall (Berven 1990). Therefore, these values were drawn in pairs in the wood frog model so that, for example, a year with high 1-year-old survival also had high 2-year-old survival. Because the salamander model included only one adult age class, adult survival was inherently correlated in this model.

Wood frog fecundity was calculated by converting life-table data from Berven (1990) directly into postbreeding matrix elements. Spotted salamander fecundity was calculated with the following equation: $f = a^*b^*c^*0.5$, where a is adult survival (because the model is a postbreeding model and individuals must survive to the next year to breed), b is breeding frequency (because not all mature females breed each year), c is clutch size (clutch size is multiplied by 0.5 with the assumption that half of the clutch is female, Shoop 1974). Fecundity was calculated during the salamander simulations with randomly selected values of adult survival, breeding frequency [range 0.75–0.90 (Whitford & Vinegar 1966; Blackwell et al. 2004)], and clutch size of 224 (Shoop 1974).

Juvenile survival for spotted salamanders is difficult to estimate because juveniles cannot easily be relocated on an annual basis. Our estimate of 0.76 for juvenile survival was inferred by determining the value required to yield a stochastic log growth rate of 1 after all other matrix elements had been parameterized with published data. This estimate is reasonable assuming probabilities of juvenile survival are higher than survival in the first year after metamorphosis, but not as high as adult survival. We also calculated the stochastic log growth rate of the parameterized wood frog model and made minor adjustments to the frequencies at which survival estimates were drawn to yield a stochastic log growth rate of 1 (Table 1). This ensured that both the wood frog and spotted salamander models began with a population that was neither growing nor declining before running simulations with reductions in habitat.

Estimating Distribution of Individuals in the Terrestrial Habitat

Predicting the effects of loss of terrestrial habitat on amphibian population persistence requires knowing how many individuals will be affected when habitat is lost. To estimate the proportion of the population occurring within a given distance of wetlands, we used the univariate kernel density estimates of space-use for frogs and salamanders reported in Rittenhouse and Semlitsch (2007). These estimates were based on 13 radiotelemetry studies of adult pool-breeding amphibians and showed that frogs use habitat at distances farther from the wetland than salamanders during the nonbreeding season. To estimate the proportion of the population occurring within a given radius of the wetland, we summed the raw-kernel density estimate at 2.5-m intervals from the wetland to the distance of interest and divided this number by the sum of the raw-kernel density estimates at 2.5-m intervals from the wetland to 1000 m (Table 3). On the basis of these estimates, we assumed that 100% of wood frogs and spotted salamanders in a population occur within 1000 m and 290 m of the wetland, respectively (Table 3). Although greater distances have been reported, telemetry studies place most adults well within these ranges.

We ran simulations for wood frogs with 9 different sizes of terrestrial habitat area ranging from 30 to 1000 m from the breeding pool and for spotted salamanders with 8 different sizes of terrestrial habitat ranging from 5 to 290 m from the breeding pool. For both species these ranges encompassed from 7 to 100% of individuals in the population, meaning that 0 to 93% of individuals were affected by reductions in habitat. We assumed the distribution of juveniles in the terrestrial habitat was equivalent to that of adults. Limited data suggest juvenile wood frogs and spotted salamanders do not migrate farther from wetlands than adults, but that juvenile wood frogs typically migrate farther than juvenile spotted salamanders (Patrick et al. 2006; Patrick et al. 2008). Males and females were assumed to be affected equally; however, we did run one set of simulations with limited data that suggest female wood frogs and spotted salamanders may migrate farther from breeding sites than males.

Table 3. Estimates of the proportion of the population of frogs and salamanders that use terrestrial habitat within a given radius of the wetland and estimates of maximum terrestrial female population size (carrying capacity) used in model projections.*

	Radius (m)	*Density*	*Cumulative density*	*Proportion of population*	*Carrying capacity*
Frogs	30	0.0023	0.0258	0.074	76
	50	0.0025	0.0453	0.129	133
	100	0.0027	0.0986	0.281	290
	165	0.0022	0.1627	0.463	479
	290	0.0011	0.2438	0.694	717
	340	0.0008	0.2630	0.749	774
	500	0.0006	0.3046	0.867	896
	750	0.0002	0.3403	0.969	1001
	1000	0.0001	0.3512	1.000	1033
Salamanders	5	0.0099	0.0268	0.073	11
	10	0.0112	0.0487	0.132	20
	20	0.0113	0.0949	0.257	38
	30	0.0091	0.1351	0.365	55
	50	0.0053	0.1887	0.510	77
	100	0.0026	0.2628	0.710	107
	165	0.0024	0.3251	0.879	132
	290	0.0004	0.3684	0.996	149
	1000	0.0000	0.3699	1	150

**We report the raw density estimate (density) and the cumulative sum of density estimates from the wetland out to a given radius (cumulative density), extracted from univariate kernel density estimates published in Rittenhouse and Semlitsch (2007). These estimates were used to estimate the proportion of the population within each habitat area and reductions in terrestrial carrying capacity.*

Model Projections

Initial wood frog and spotted salamander population vectors were drawn randomly in specified proportions from a range of population size estimates on the basis of egg mass surveys of 124 ponds in Rhode Island that ranged in size from 0.003 to 1.509 ha (Egan & Paton 2004). We included carrying capacity in the model as a ceiling, which restricted the maximum number of females in the population. We based estimates of the maximum size of a breeding population on Egan & Paton's (2004) counts of egg masses and set wood frog and spotted salamander carrying capacities at 1033 and 250 adult females, respectively. We used these values in the model when terrestrial core habitat encompassed 100% of the adult breeding population and reduced them proportionally according to the number of individuals affected by reductions in terrestrial core habitat (Table 3).

For each simulation we ran 30 iterations, each of which consisted of 5000 replications in which the population was projected forward 20 or 60 years. Model output included extinction probabilities for each year (mean from the 30 iterations) and mean and median adult female population sizes at the end of each simulation. In all simulations populations were considered extinct if at any time during the simulation no adult females remained in the population. All model simulations assumed that individuals outside the suitable terrestrial habitat die in the first year that habitat is lost and that carrying capacity is reduced in subsequent years. We ran 4 sets of model simulations that differed in their assumptions regarding degree of habitat degradation, distribution of males and females in the terrestrial habitat, and rates of immigration.

The first set of simulations assumed that habitat quality within the remaining forested terrestrial habitat was not degraded (e.g., no edge effects) and included areas suitable for summer foraging and overwintering; therefore, adult survival rates within this area were not reduced. These simulations also assumed that loss of surrounding forested habitat resulted in isolation of the population, which eliminated the possibility of immigration. To allow comparisons of wood frog and spotted salamander model predictions for a similar number of generations and the same number of years, we ran spotted salamander simulations for 60 and 20 years. Simulations of 20 years for wood frogs and 60 years for spotted salamanders equate to roughly 10–20 generations.

In a second set of simulations, we tested the sensitivity of model predictions to the assumption of equal distributions of males and females in the terrestrial habitat. Results of several studies show that female pond-breeding amphibians migrate farther from wetlands than males, which suggests that buffer zones that are too small could disproportionately affect females (reviewed in Rittenhouse & Semlitsch 2007). Although available data are insufficient to develop female-specific kernel-density estimates of space use for wood frogs and spotted salamanders, the proportion of females in a population that overwinter beyond specific distances have been estimated in 3 studies. For wood frogs we ran simulations with a terrestrial habitat size of 65 m from the wetland that affected 87.5% of females in the population (Regosin et al. 2003*a*), rather than 77% of females as in our other simulations. We ran salamander simulations with 65 m of habitat that affected 87% of females (Regosin et al. 2003*b*), rather than 40%, and simulations with 100 m of habitat that affected 51% of females (Windmiller 1996), rather than 29%. These models assumed no immigration and no habitat degradation.

A third set of projections estimated the sensitivity of extinction probabilities to habitat degradation. Because there were insufficient data to estimate the effects of habitat degradation on terrestrial survival rates or to estimate the effects of reductions in specific habitat types (i.e., overwintering vs. summer foraging), we ran simulations for a range of habitat-degradation scenarios, with survival rates of all terrestrial life-history stages reduced in 5% increments from 0 to 25%.

A fourth set of models estimated the sensitivity of extinction probabilities to a range of immigration rates. The natural fluctuations in population size of pond-breeding amphibians suggest that these populations may depend on immigration for long-term persistence (Pechmann et al. 1991). Studies of allele frequencies document substantial gene flow among wood frog (Newman & Squire 2001) and spotted salamander populations (Zamudio & Wieczorek 2007), which suggests that immigration is a common occurrence. We ran simulations with annual probabilities of successful immigration ranging from 0.10 to 0.5. During model projections 5, 1-year-olds (wood frogs) or 5 juveniles (spotted salamanders) were added to the population vector in years that were randomly selected as having successful immigration.

Results

No Habitat Degradation or Immigration

Loss of terrestrial habitat, modeled as an initial reduction in population size and a permanent reduction in carrying capacity, resulted in increased extinction probabilities (Fig. 1) and decreased mean and median population sizes for wood frogs and spotted salamanders. Extinction probabilities for wood frogs were much higher than for spotted salamanders when there was no habitat loss (i.e., a 1000-m radius of terrestrial habitat around the wetland for wood frogs and 290 m for spotted salamanders). In this scenario, environmental stochasticity resulted in an 11% probability of extinction for wood frog populations

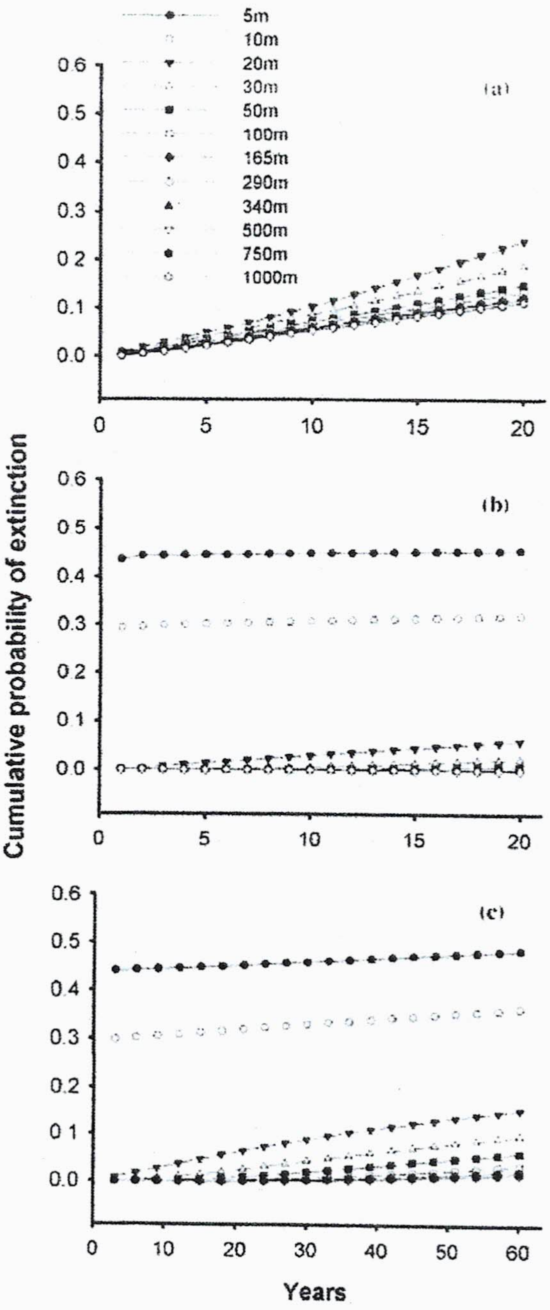

Figure 1. Results of model simulations predicting the probability of extinction of (a) wood frog populations within 20 years with terrestrial habitat areas ranging from 30 to 1000 m from the breeding site and spotted salamander populations within (b) 20 years and (c) 60 years with terrestrial core-habitat areas ranging from 5 to 290 m from the breeding site. Model simulations assumed mortality of all individuals outside the suitable terrestrial habitat area in the first year and a reduction in carrying capacity in subsequent years.

within 20 years and only a 0.02% probability of extinction for spotted salamanders. When we simulated spotted salamander populations for 60 years to compare the 2 species across similar numbers of generations, salamanders had a 1.7% probability of extinction without habitat loss, still substantially less than for wood frogs (Fig. 1). Nevertheless, probabilities of spotted salamander extinction were much higher (45% within 20 years and 48% within 60 years) than those of wood frogs (24% within 20 years) when terrestrial habitat was reduced such that 93% of each population experienced mortality in the first year of the simulation. The species also differed in that cumulative extinction probabilities increased rapidly over time for wood frogs, but at a much slower rate for spotted salamanders (Fig. 1). Population sizes declined linearly with reductions in terrestrial habitat (wood frogs: $y = -266x + 270$; salamanders: $y = -31x + 35$, where y is median population size after 20 years and x is proportion of population experiencing mortality in the first year of the simulation).

Sensitivity to Assumption of Equal Distribution of the Sexes

Simulations with a 65-m radius of terrestrial habitat around a pond in which females were assumed to migrate farther from breeding ponds than males resulted in minor differences in model predictions for wood frogs (19% vs. 16% probability of extinction within 20 years), but dramatically different predictions for spotted salamanders (32% vs. 0.3% probability of extinction within 20 years). With a habitat radius of 100 m, however, differences in extinction probabilities were relatively minor for spotted salamander models that assumed unequal and equal distributions of the sexes (0.8% vs. 0.2% probability of extinction within 20 years).

Sensitivity to Habitat Degradation

In simulations that included habitat degradation (modeled as reductions in terrestrial survival rates) extinction probabilities increased for both species, but at a far greater rate for spotted salamanders than for wood frogs (Fig. 2). With only a 5% reduction in terrestrial survival rates of spotted salamanders, extinction probabilities more than quadrupled (from 6 to 25% within 20 years) for populations with 20 m of terrestrial habitat and increased nearly 2 orders of magnitude for populations that did not experience habitat loss (from 0.028 to 2.2% within 20 years). When terrestrial survival rates were reduced by 25%, all salamander populations reached extinction within 20 years. The same 25% reduction in terrestrial survival in wood frog simulations more than doubled extinction probabilities, with a maximum probability of extinction of 58% within 20 years (Fig. 2).

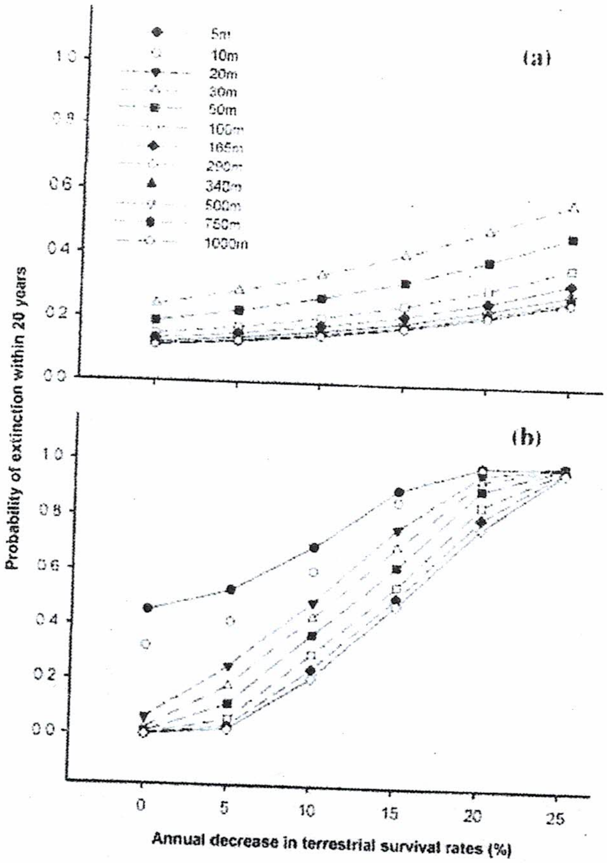

Figure 2. Predicted increases in probability of extinction of (a) wood frog and (b) spotted salamander populations within 20 years when habitat loss is accompanied by reductions in terrestrial survival rates for individuals in the remaining terrestrial habitat. Results are shown for a range of terrestrial core-habitat sizes identified in the legend.

Sensitivity to Immigration Frequencies

Wood frog extinction probabilities were substantially reduced in simulations with successful immigration (Fig. 3). When habitat area was unaltered, frequent immigration decreased wood frog extinction probabilities from 11 to 3%. When the terrestrial habitat radius was reduced to 30 m, frequent immigration decreased wood frog extinction probabilities from 24 to 5%. When annual probabilities of immigration were 0.25 or greater, the already low extinction probabilities of spotted salamanders were decreased to 0 in simulations with no habitat reduction. Immigration did not substantially reduce high probabilities of spotted salamander extinction in simulations with 5 m of terrestrial habitat.

Immigration resulted in increased population sizes for wood frogs and spotted salamanders, but proportionally had a greater effect on spotted salamander numbers (Fig. 3c & 3d). When habitat area was not reduced and annual probabilities of immigration were high, spotted salamander median population size increased by 63% (from 19 to 31), whereas the median population size of wood frogs increased by 25% (from 148 to 185).

Discussion

Our simulations predicted increased risk of decline and extinction for wood frog and spotted salamander populations with the loss of terrestrial habitat surrounding breeding sites. Simulations in which populations were isolated, terrestrial habitat was reduced to 30 m or less (still larger than most buffer zones enforced by current policies), and survival was only reduced by 5% (an extremely low reduction) predicted spotted salamander declines of 80% in median population size and an 18% probability of extinction within 20 years. For the more vagile wood frogs, the predicted effects of applying this buffer width were even greater, with declines of 94% in median population size and a 29% probability of extinction within 20 years. Our simulation results clearly suggest that 30 m of terrestrial habitat around isolated wetlands is insufficient to maintain viable populations of wood frogs or spotted salamanders, especially when habitat quality is reduced by surrounding land-use practices as is often the case in regulated buffer zones (Semlitsch & Jensen 2001).

Although most pool-breeding amphibians in the northeastern United States use more than 30 m of terrestrial habitat around breeding sites, the area of habitat required depends on whether the goals of a particular policy focus on extinction risks or maintenance of ecosystem function. For example, a population of wood frogs or spotted salamanders may have a relatively low probability of extinction with a terrestrial habitat radius of 50 m, assuming the quality of the habitat remains high, but these populations will likely be reduced to less than half their original size. These smaller populations are subject to additional extinction risks, including increased susceptibility to the effects of catastrophes, disease, genetic drift, and demographic stochasticity.

Reduced amphibian population sizes have the potential to drastically alter the integrity of wetland ecosystems by disrupting the complex interactions among wetland organisms. For example, tadpoles can be important ecosystem engineers in aquatic systems, exerting top-down control of algae and periphyton (Mallory & Richardson 2005). Without herbivorous tadpoles, excessive algal growth may cause eutrophication, which typically leads to reduced wetland biodiversity (Bedford et al. 2001). Carnivorous salamander larvae also play an important role, acting as top predators in many fishless wetlands

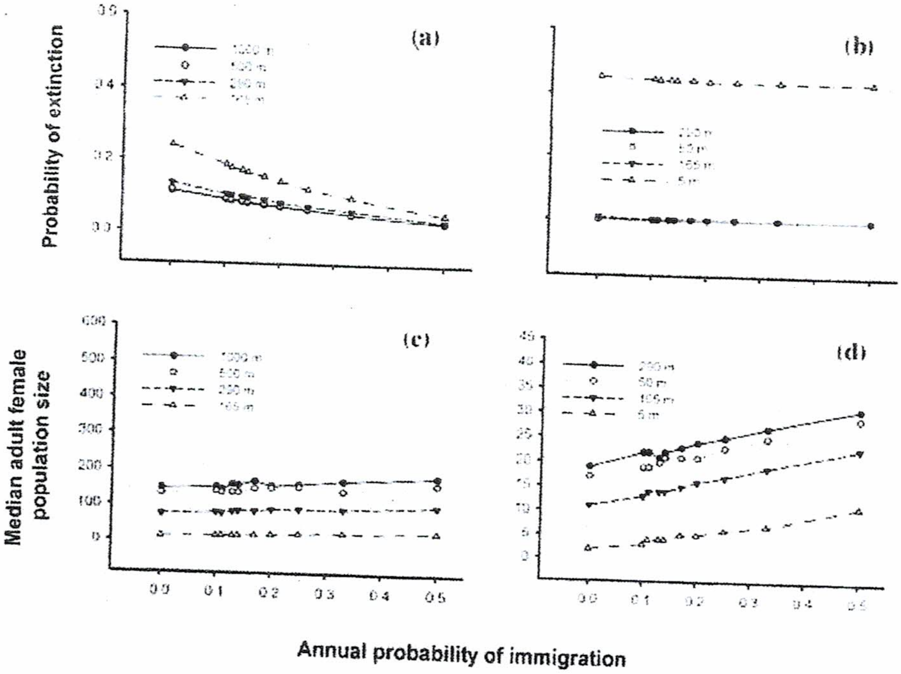

Figure 3. Effects of the frequency of successful immigration on the predicted probability of extinction within 20 years for (a) wood frogs and (b) spotted salamanders and on the median population size after 20 years for (c) wood frogs and (d) spotted salamanders. Results are shown for a range of terrestrial core-habitat sizes identified in the legend.

(Holomuzki & Collins 1987). Following metamorphosis, these amphibians provide an important link between aquatic and terrestrial systems through the transfer of energy and nutrients (Regester et al. 2005). Some isolated wetlands can produce as much as 1400 kg of amphibian biomass in a single breeding season (Gibbons et al. 2006), providing a substantial prey base for a wide range of terrestrial vertebrates. As insectivorous adults, amphibians consume and potentially regulate invertebrate detritivore populations in forested ecosystems and may be important in stabilizing rates of decomposition (reviewed in Davic & Welsh 2004). Although there is still much to be learned about the role of amphibians in wetland systems, it is clear that amphibian declines and extinctions have consequences beyond the loss of a single population or species.

To maintain populations of spotted salamanders with a 95% probability of persistence over 20 years, our models indicated that a minimum terrestrial core-habitat radius of between 100 and 165 m is required, assuming sufficient habitat quality is maintained to prevent reductions in terrestrial survival rates of greater than 5%. The area within 165 m of the breeding site should be considered core habitat and an additional buffer zone should be in place to ensure the core-habitat quality remains high (Semlitsch & Jensen 2001). The importance of high-quality terrestrial habitat for spotted salamander populations was emphasized in our simulations by their high sensitivity to changes in terrestrial survival rates. This sensitivity is typical for species with long life spans and delayed reproductive maturity (Congdon et al. 1994). Even with sufficient terrestrial habitat to encompass 100% of the adult population, spotted salamanders in our simulations experienced extinction probabilities of nearly 50% when survival was reduced by 15%. Therefore, wetland policies—such as the recent amendments to Massachusetts' Wetlands Protection Act—that require a 30-m (100-foot) buffer zone around wetlands but allow construction within the outer 15.2 m (50 feet) and as much as 40% impervious surface are likely to erode habitat quality within wetland buffer zones and make local extinctions of salamander populations much more likely.

For wood frogs our models indicated that maintaining a high probability of persistence requires not only adequate terrestrial habitat but also sufficient connectivity with other breeding populations. Extinction probabilities within 20 years were over 5% for wood frogs even with a habitat radius that encompassed the entire population and with high-quality habitat that did not reduce adult survival. This result suggests that isolating wood frog populations from the possibility of recolonization will likely result in localized extirpations and regional decline. These conclusions are supported by the results of landscape-scale studies that show isolated populations of wood frogs are highly susceptible to stochastic extinction (Gibbs 1998; Squire & Newman 2002). Current policies regulating development near wetlands do not address the issue of maintaining connectivity among small wetlands. For amphibians breeding in isolated wetlands, the opportunity for successful immigration is essential to the maintenance of viable populations.

Our model results support the conservation recommendations of previous studies emphasizing the importance of sufficient high-quality terrestrial core habitat and connectivity for the maintenance of pool-breeding amphibian populations (e.g., Trenham & Shaffer 2005). Our knowledge of the terrestrial ecology of these amphibians is limited, and additional studies would certainly improve the precision of our model predictions. Our simulations that explored the implications of females migrating farther than males underscore the need for further study of sex-specific habitat requirements. Despite limited data we are confident in the conclusion that the maintenance of wetland biodiversity requires the protection of terrestrial habitat far beyond a 30-m buffer zone. Although maintaining a 165- to 200-m radius of high-quality terrestrial core habitat around all amphibian-breeding sites may not be feasible, some conservation strategies, such as the "best development practices" described by Calhoun et al. (2005), allow for the preservation of high-quality wetlands and adjacent habitat and allow development to proceed near degraded wetlands that no longer provide suitable wildlife habitat.

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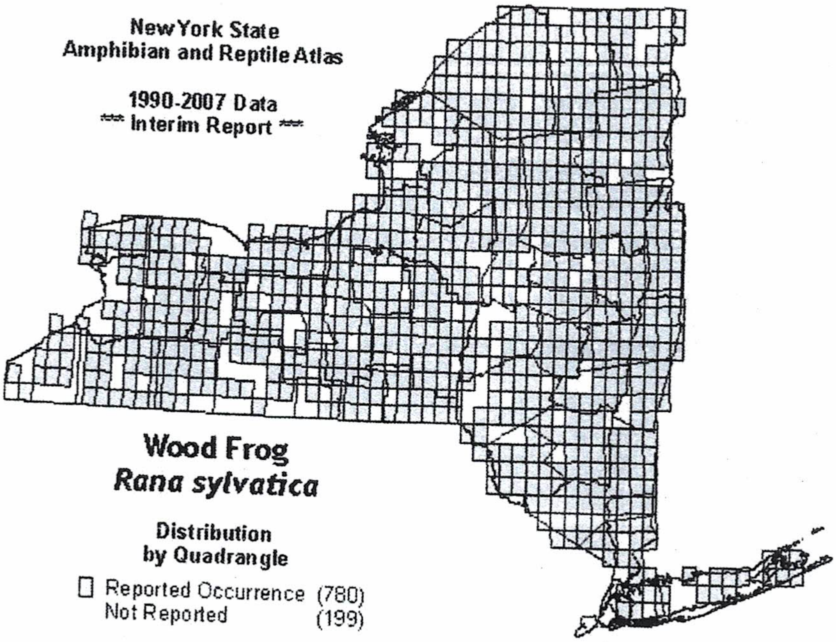
Wood Frog Distribution Map



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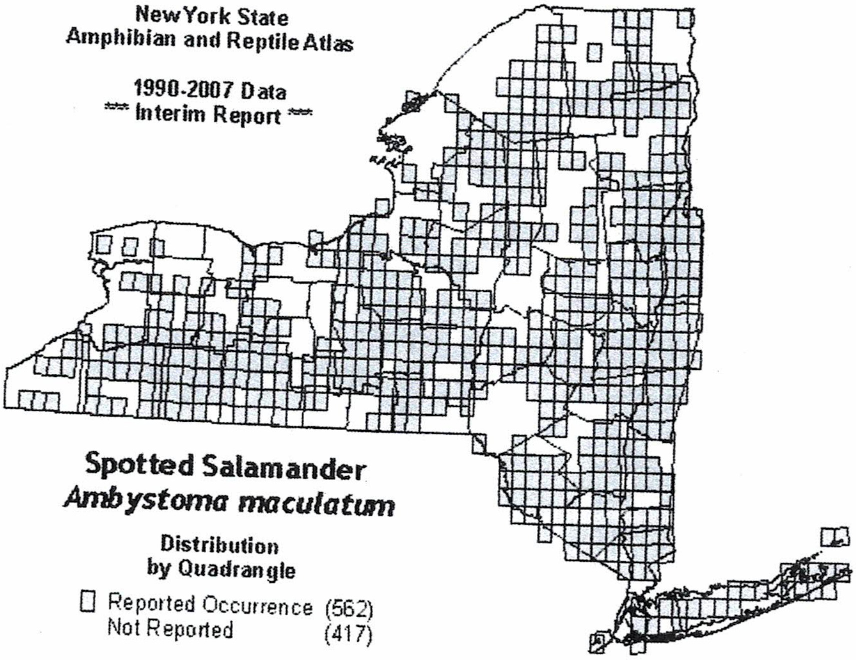
Spotted Salamander Distribution Map



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