The significance of hydroperiod and stand maturity for pool-breeding amphibians in forested landscapes

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Abstract: The loss of small seasonal wetlands and adjacent forested habitat is a major threat to pool-breeding amphibians in North America. Identifying environmental correlates of breeding effort (and success) in remaining intact landscapes is a critical first step in conservation planning. Little is known about how pool-breeding amphibian populations respond to fine-scale variations in hydroperiod or neighboring forest structure and composition. We studied these associations for wood frogs (*Rana sylvatica* LeConte, 1825) and spotted salamanders (*Ambystoma maculatum* (Shaw, 1802)) in a forested New England landscape (southern Maine, USA). We conducted egg mass counts across two seasons at 87 strictly seasonal pools. The influence of hydroperiod and landscape (150 and 500 m scales) habitat characteristics on breeding effort were investigated. Pools with longer hydroperiods (\geq 18 weeks post breeding) that were relatively isolated from other breeding wetlands (<13 neighboring pools within 150 m and <19 within 500 m) supported larger breeding populations of both wood frogs and spotted salamanders. Salamander breeding populations were largest in relatively mature forests. Naturalized, anthropogenic pools supported comparable levels of breeding effort with that of natural pools. Conservation planning for wood frogs and spotted salamanders should incorporate pools at the longer end of the seasonal hydroperiod gradient.

Résumé: La perte des petites terres humides saisonnières et des habitats forestiers adjacents en Amérique du Nord est une menace majeure pour les amphibiens qui se reproduisent dans les étangs. L'identification des variables en corrélation avec l'effort (et le succès) reproductif dans les paysages intacts qui restent est une première étape essentielle dans la planification de la conservation. On connaît mal comment les populations d'amphibiens qui se reproduisent dans les étangs réagissent aux variations à échelle fine de l'hydropériode ou de la structure et de la composition de la forêt avoisinante. Nous avons étudié ces associations chez la grenouille des bois (Rana sylvatica LeConte, 1825) et la salamandre maculée (Ambystoma maculatum (Shaw, 1802)) dans un paysage forestier de la Nouvelle-Angleterre (sud du Maine, É.-U.). Nous avons dénombré les oeufs durant deux saisons dans 87 étangs strictement saisonniers. Nous avons évalué l'influence de l'hydropériode et des caractéristiques d'habitat du paysage (à des échelles de 150 m et de 500 m) sur l'effort reproductif. Les étangs à hydropériode plus longue (>18 semaines après la reproduction) qui sont relativement isolés d'autres terres humides de reproduction (<13 étangs adjacents dans un rayon de 150 m et <19 étangs dans un rayon de 500 m) contiennent des populations reproductrices plus importantes à la fois de grenouilles des bois et de salamandres maculées. Les populations reproductrices de salamandres sont plus importantes dans les forêts relativement matures. Les étangs naturalisés et anthropiques permettent un effort reproductif comparable à celui dans les étangs naturels. La planification de la conservation des grenouilles des bois et des salamandres maculées devrait tenir compte des étangs qui se situent dans la partie des hydropériodes les plus longues du gradient des durées d'hydropériodes saisonnières.

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Introduction

Many pool-breeding amphibians have complex life histories that require both aquatic and terrestrial habitat to support

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 ²Present address: Department of Forestry and Natural Resources, Clemson University, 261 Lehotsky Hall, Clemson, SC 29634-0317, USA. distinct larval and adult life-history phases (Wilbur 1980; Semlitsch 2000). Previous research provides strong evidence that amphibian larval development and community structure in seasonal pools (pools that periodically dry) is significantly affected by factors operating at the scale of the breeding pool — especially hydroperiod (duration of inundation), which influences interspecific competition (Wilbur 1972, 1997; Relyea 2004), predation (Wilbur 1972; Petranka et al. 1998; Relyea 2003), growth and development (Rowe and Dunson 1995), and attendant interactions (reviewed by Wellborn et al. 1996; Semlitsch 2000). Dispersing juveniles and migrating adults of most pool-breeding amphibians are also dependent on terrestrial habitat for foraging and overwintering (Semlitsch 1998; Regosin et al. 2003a; Semlitsch and Bodie 2003). Conservation planning for pool-breeding amphibians thus must be informed from habitat investigations at multiple scales - mainly pool (i.e., breeding and

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development), local (i.e., foraging, migration, and overwintering), and landscape (i.e., dispersal) scales (Marsh and Trenham 2001; Semlitsch 2002; Porej et al. 2004).

At the wetland scale, hydroperiod is primary among the abiotic factors responsible for structuring community composition and breeding success of pool-breeding fauna (Pechmann et al. 1989; Semlitsch et al. 1996; Snodgrass et al. 2000; Babbitt et al. 2003). Generally, shorter hydroperiod wetlands favor species characterized by rapid development and low tolerance for predation, while longer hydroperiod wetlands favor those species with slower development and greater adaptations for predation (reviewed by Semlitsch 2000). Patterns of hydroperiod-faunal relationships described in most studies are based on a wide range of wetland hydroperiods, from seasonal to permanent, documenting the occurrence of populations versus more sensitive measures of breeding population response (Snodgrass et al. 2000; Babbitt et al. 2003; Kolozsvary 2003). Remaining less understood are the effects of hydroperiod variability on amphibian populations within strictly seasonal portions of the inundation continuum (Pechmann et al. 1989; Rowe and Dunson 1995). By focusing solely on isolated, seasonal wetland systems and two species that commonly breed there, the wood frog (Rana sylvatica LeConte, 1825) and the spotted salamander (Ambystoma maculatum (Shaw, 1802)), we hope to better understand the significance of fine-scale hydroperiod variability in a wetland type that has been identified among the most threatened in North America (Tiner 1999; Colburn 2004).

At the same time, breeding pool habitat characteristics need to be evaluated in the context of local forest and landscape suitability as post-breeding habitat for adults and dispersing juveniles. Evidence is growing that forest poolbreeding amphibians, such as the wood frog and spotted salamander, use preferentially closed canopy forest conditions during post-breeding movements and periods of summer and winter activity (deMaynadier and Hunter 1995, 1998; Gibbs 1998; Rothermel and Semlitsch 2002; Faccio 2003; Baldwin 2005). Such nonbreeding habitat preferences by amphibian species with limited, albeit impressive, migration capabilities (Semlitsch and Bodie 2003) suggest that finescale differences in forest structure and composition surrounding breeding wetlands can have important effects on the presence and size of local breeding populations. Although these behavioral associations are well known, few published studies have investigated general forest extent at multiple spatial scales (Egan 2001; Homan et al. 2004; Porej et al. 2004; Rubbo and Kiesecker 2005). A number of studies have examined the effect of urbanization or forest fragmentation on amphibian population patterns (Gibbs 1998; Kolozsvary and Swihart 1999; Rubbo and Kiesecker 2005), but none has investigated fine-scale forest habitat variables in intact landscapes in relation to breeding population size. Working in intact forested systems allows us to evaluate the relative importance of both pool and adjacent habitat quality to amphibian breeding populations. This information could inform conservation strategies of seasonal pools by identifying finer scale habitat conditions important to pool-breeding amphibians.

To this end, we investigated the importance of pool hydroperiod and terrestrial habitat characteristics at two spatial scales (150 and 500 m) on breeding population size of two North American amphibians that breed primarily in seasonal pools. In conducting our study in a mostly forested landscape, we hoped to identify optimal breeding and postbreeding habitat conditions prior to the confounding effects of wide-scale forest fragmentation. Our specific study objectives were to (*i*) quantify pool occupancy based on egg-mass counts, (*ii*) investigate potential effects of fine-scale differences in hydroperiod on breeding effort, and (*iii*) model the relative importance of hydroperiod and terrestrial habitat characteristics on annual amphibian breeding effort in a relatively undisturbed forested landscape.

Materials and methods

Study area

We selected three southern Maine towns — North Berwick (98.8 km²), Biddeford (78.4 km²), and Kennebunkport (52.5 km^2) (Fig. 1) — as representative of the forest, wetland, and land-use patterns of southern Maine. Although bio-physically similar to southern and central New England, and hosting similarly high wetland densities (Calhoun et al. 2003), southern Maine forests remain relatively intact. The urbanizing land-use pattern is characterized by a forested landscape that is fragmented by (i) scattered, low-density residential developments; (ii) secondary rural roads; (iii) light selective forestry; and (iv) abandoned fields (Baldwin 2005). The forests were cleared extensively for agriculture by the early 20th century (Foster 1992; Russell et al. 1993) and, following a severe burn in 1947, much of this area was abandoned and left to regenerate to forest (Butler 1987; Copenheaver et al. 2000). Presently, the postburn forest is dominated by mid-successional oaks (northern red oak, Quercus rubra L., and white oak, Quercus alba L.) and the unburned forest by late-successional American beech (Fagus grandifolia Ehrh.), birch (genus Betula L.), eastern hemlock (Tsuga canadensis (L.) Carr.), and red oak.

Pool selection

We delineated potential seasonal breeding pools (N = 365) using color infrared (CIR) stereo photography (1:12000 scale, spring 2000 leaf-off). One hundred and sixty-five pools were randomly selected and stratified to ensure coverage in proportion to pool density in each of the study towns. We used tax parcel data to seek private-property access from 88 individual landowners and 49% granted permission for access. Delineated pools were field-checked prior to final selection to ensure that they were seasonal pools in forested settings. We used hydrophytic, soil, connectivity, and geomorphic criteria to establish seasonality. We selected for study 87 pools distributed among study towns as follows — North Berwick: 23 pools; Biddeford: 25 pools; and Kennebunkport: 39 pools.

Breeding population assessment

We conducted egg-mass counts at each of the breeding pools during 2002 and 2003, with two successive counts per season. The first count in early April was timed immediately following the peak of wood frog breeding activity and the second count in late May was timed to capture later breeding waves by spotted salamanders (Petranka 1998). We 1606

Fig. 1. Southern Maine study area and the distribution of aerially delineated potential breeding pools (n = 365), and those selected for inclusion in the study (n = 87), within three largely forested study towns. Portland, Maine's largest metropolitan center (population of 62 878), is approximately 48.3 km northeast of Biddeford.



counted egg masses by slowly wading through the entire pool area while counting individual masses visually or, if layered below the surface, by feeling and counting manually. To ensure that we did not double-count masses, the location and number of egg masses for each species were located on a fine-scale map of each pool relative to local features such as branches, trees, and hummocks.

Breeding-pool parameters

We measured hydroperiod using Hobo[®] H8 temperature data loggers set to record hourly temperature. Loggers were fastened with stakes to the bottom of pools, at the deepest estimated location, during spring high water and removed after pools began to recharge in late fall. We downloaded temperature profiles (Onset Computer Corporation, Inc., Bourne, Massachusetts) to estimate pool-drying date by noting the onset of air (versus water) temperature signals and of pronounced night-day cyclical temperature variation. We then characterized hydroperiod as the number of weeks between the onset of breeding in the study area (normalized as 1st of April) and the estimated pool drying date.

Three hydroperiod thresholds were constructed based on amphibian developmental rates. Wood frog average developmental period (egg-mass deposition to metamorphosis) of 12.5 weeks (Hunter et al. 1999) defined the shortest hydroperiod threshold for both species. The spotted salamander's average developmental period of 18 weeks (Petranka 1998) defined the longest hydroperiod threshold. The third and final period — intermediate — was defined as 16 weeks, corresponding to low spotted salamander and high wood frog developmental period estimates (Petranka 1998; Hunter et al. 1999; see also Paton and Crouch 2002) and similar to an "intermediate" period used in related studies (Babbitt et al. 2003; Babbitt 2004). A goodness-of-fit χ^2 test was used to

determine if egg-mass numbers of both species occurred in greater or lesser than expected numbers given the availability of pools in each hydroperiod category.

We calculated pool area (m²) in the field by dividing the pool into polygons and measuring their legs, subsequently calculating their areas and cumulatively adding them to achieve pool area. Pool depth (cm) was taken at the deepest point at early-spring, high water. A hemispheric, digital photograph of the canopy was taken at pool center with a Nikon Coolpix 990 camera and fisheye lens and analyzed for the percentage of canopy openness (Frazer et al. 1999). We noted whether a pool was of artificial origin, or historically altered (e.g., berms, dams, ditches, culverts), permitting goodness-of-fit analyses of breeding effort between natural and anthropogenic pools.

Terrestrial habitat

Two radial spatial scales — 150 and 500 m — were used to assess the terrestrial habitat surrounding breeding pools. We chose to survey within the 150 m distance because this distance reflects a plausible pool-breeding amphibian "life zone" for adult wood frogs and spotted salamanders (Gordon 1968; Madison 1997; Semlitsch 1998; Semlitsch and Bodie 2003). For example, Semlitsch (2000) recommends a core conservation zone for pool-breeding amphibians of 164 m from breeding pools.

We classified forest cover types as mixed, deciduous, coniferous, and wet forest and required a minimum area of 0.15 ha within the 150 m radius to be considered for sampling. We randomly placed circular plots (0.05 ha) within a 150 m radius of each pool (~7 ha) and stratified by area of each major forest cover type (determined through aerial photography) to assess forest characteristics. We assessed three plots per cover type. Species and diameter at breast height (DBH) for every tree >10 cm DBH were recorded. We used total basal area to characterize forest stand density (Husch et al. 1982; Barnes et al. 1998).

Downed woody material (DWM) >10 cm diameter was classified by degree of decomposition in 1 of 4 decay classes (Fraver et al. 2002). Volume of DWM was calculated using methods provided in Fraver et al. (2002) and converted to volume per decay class per hectare per breeding pool for analysis. Presence of burn scars and saw cuts on each piece of DWM and standing tree was recorded.

To assess canopy cover, we took two nonoverlapping, hemispheric, digital photographs of the canopy in each plot and analyzed for the percentage of canopy cover (Frazer et al. 1999). Slope, area of rocky outcrop, and the percentage of cover of shrubs in a 5 m radius from the plot center were also estimated for each circular plot. We also took four measurements of leaf-litter depth (cm) and counted the number of potential spotted salamander burrows (>2 cm diameter and 8 cm long) in four regularly distributed 1 m × 2 m subplots.

We reduced forest variables described above, through principal components analysis (PCA), for use in regression analysis and model selection. Forest-variable loadings on PC1 and PC2 were used to characterize forest composition and structure gradients. Biplot scores of the breeding pools (i.e., samples) on the forest composition and structure gradients were then used as independent variables in regression analysis (ter Braak and Smilauer 2002).

We assessed land-use intensity (LUI), density of neighboring delineated potential breeding pools, and area of neighboring freshwater wetlands at both the 150 and 500 m scales. A 500 m radial distance was chosen to reflect a plausible anuran terrestrial habitat zone based on adult migratory distances (Lamoureux and Madison 1999; Regosin et al. 2003*a*; Semlitsch and Bodie 2003; Baldwin 2005) and to encompass a proposed conservation core zone for anurans of 368 m suggested by Semlitsch (2002). Maximum travel distances of most adult wood frogs and ambystomatid salamanders are also in this range. Neighboring wetland information was obtained for potential breeding pools from the 1:12 000 scale CIR photo-delineated set (n = 365) and for other freshwater wetlands from U.S. Fish and Wildlife Service National Wetland Inventory (NWI) maps.

We used 1:12000 scale CIR photos as the base for manually digitizing and subsequently classifying LUI polygons (Table S1).³ The minimum polygon created was the size of an average house footprint in our data set, about 0.5 ha. Following the "continuum approach" described in Sanderson et al. (2002), LUI values were assigned to each of eight classified land uses and six road classes. Assigned LUI values were inferred from specific investigations of amphibian landscape permeability (deMaynadier and Hunter 1998; Gibbs 1998; deMaynadier and Hunter 1999, 2000; Rothermel and Semlitsch 2002), as well as more general studies of amphibian habitat relationships (Shoop 1965; Means et al. 1996; Windmiller 1996; Madison 1997; Faccio 2003; Regosin et al. 2003a). Road coverage and use intensity classifications (USGS 1:24000 scale) were obtained from the state of Maine Office of GIS (http://musashi.ogis.state.me.us). Finally, LUI and road maps were converted to 100 m scale grids and added together to produce a final 1-16 LUI index. Because amphibian land-use permeability relationships are not well known, we assumed that LUI effects increase linearly along the 1-16 scale, and we estimated that LUI effects reach an asymptote (Sanderson et al. 2002) at the maximum value of 16 (i.e., urban areas in combination with large highways). A weighted average of grid cell values for LUI within each scale (150 and 500 m) for each breeding site was then calculated using

$$\frac{\sum_{n} w_i Y_i}{\sum_{n} w_i}$$

where w_i is the area of grid cell *i* and Y_i is the LUI value at grid cell *i*.

Regression analysis and model selection

Egg-mass counts were used as the response variable, indicating local breeding population size in multiple negative bi-

³ Available on the journal Web site (http://cjz.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 5096. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

nomial regression and model selection using Akaike's information criterion (AIC), to identify the best combinations of environmental variables associated with breeding population counts (White and Bennetts 1996; Burnham and Anderson 2002). Analyses were conducted in SYSTAT[®] version 11 (Systat Software Inc. 2004) using the following loss function:

$$-1\{\log\gamma(\theta + \text{count}) - \log\gamma(\theta) - \log\gamma(\text{count} + 1) \\ + \text{count}[\log(\text{estimate})] + \theta\log(\theta) \\ - (\theta + \text{count})\log(\theta + \text{estimate})\}$$

In an effort to keep candidate model selection grounded in biological reality, candidate models (20) were formulated based on known importance of hydroperiod and to determine relative effects of terrestrial habitat variables. A literature review was conducted and a priori models that contain those variables believed to be the most important were included. Because our ratio of sample size (87) to estimated parameters (7) was low (12.4), we employed Akaike's information criterion corrected for small sample sizes (AIC_c).

Our pools occurred in 43 clusters, or groups of pools separated by <500 m (not all of the 87 pools were spatially independent). In a jackknifing procedure, we conducted 30 iterations of regression analysis, each of which contained a pool from a spatially independent pool cluster, that resulted in N = 43 for each iteration. For each iteration, AIC_c-model rankings were produced and the consistency of best approximating model rankings was assessed. For each candidate model (selected through literature review), an average AIC_c was generated from the 30 iterations.

To determine which candidate models were the most plausible, Burnham and Anderson (2002) suggest using a combination of three AIC metrics: (1) Δ AIC (Δ_I), which is the difference between AIC_c value for model *i* and the minimum AIC_c value; (2) Akaike weight (w_i), which is the "weight of evidence" in favor of model *i*; and (3) evidence ratios (w_1/w_i). Summing w_i for the top-ranked models until $\Sigma w_{i-j} = 0.95$ produces an inclusive confidence set, within which evidence ratios <3 and Δ_I <4 may be used to determine the most plausible (equally so) models.

Because the intercorrelation of year-1 and year-2 counts was significant (see Results), regression analysis and model selection were conducted on year-1 data (randomly chosen). To examine whether spotted salamander results were influenced by including potentially unrealistically short hydroperiods, 14 study pools with hydroperiods <16 weeks (plausible minimum hydroperiod derived from Petranka 1998) were omitted and regression analysis and model selection were repeated (3 iterations). Values are presented as means \pm SD and the significance level is set at $\alpha = 0.05$.

Results

Breeding population assessment

Egg-mass counts varied widely among individual pools (Table S2),³ but were highly correlated within species and between years and were significant (wood frog, year 1 to year 2: $r_{\rm S} = 0.88$; spotted salamander, year 1 to year 2: $r_{\rm S} = 0.83$). Pool occupancy rates over both years were 89.7% for spotted salamanders and 83.9% for wood frogs. There was a

positive, significant relationship between egg-mass counts of wood frogs and spotted salamanders in both years (year 1: $r_{\rm S} = 0.74$; year 2: $r_{\rm S} = 0.57$).

We elimated the blue-spotted salamander (*Ambystoma laterale* Hallowell, 1856) and the *A. laterale* × *Ambystoma jeffersonianum* (Green, 1827) complex (Hunter et al. 1999) from our analyses because our sample size of this poolbreeding species was too low to permit comparative analyses with the wood frog and spotted salamander. A total of 13 blue-spotted egg masses were detected among 7 study pools across both years for an overall presence of 8% (7/ 87 pools).

Habitat characteristics

Breeding pools

All pools in our study were seasonal, with hydroperiods ranging from 9 weeks (pool drying in early June) to 29 weeks (pool drying in early October) (Table S2).³ Pool depth (0.59 \pm 0.23 m (mean \pm SD), range 0.18–1.32 m) and pool area (801.8 \pm 776.2 m², range 13.6–5515 m²) were significantly ($\alpha = 0.05$) positively correlated with hydroperiod (depth: $r_{\rm S} = 0.449$, p < 0.05; area: $r_{\rm S} = 0.215$), but not to each other (r = 0.206). Forest canopy cover over the pools was generally closed (23.7% \pm 11.2%) and pool canopy openness was not correlated with hydroperiod ($r_{\rm S} = 0.06$).

Terrestrial habitat

Forest structure and composition

Together, principal components 1 (PC1) and 2 (PC2) were constructed from 64% of the total variation used in the first four components (46%). PC1 comprised 18.43% of the total variation of all possible components (N = 8). Variable loadings on PC1 suggest that it was primarily defined by a "forest structure" gradient, specifically stand openness and tree density (total basal area of trees and area of treeless rocky outcrops) (Table S3).³ PC2 (11.22% of the total variation) was composed primarily of variables describing tree species composition, depicting a gradient defined at one end (negative scores) by greater basal area of early successional trees (Betula populifolia Marsh., Populus tremuloides Michx., genus Prunus L.) and oaks (Quercus spp.) and a greater frequency of burn scars, and at the other end (positive scores) by mature forest, late successional indicators i.e., greater overstory presence by shade tolerant trees (F. grandifolia, T. canadensis, and Betula lenta L.) and increased volume of downed woody material (Table S3).³

Land use and wetland density

LUI values for the habitat surrounding breeding pools ranged from 1.0 (continuous forest) to 7.1 (dense residential), with a median value of 2 (open woodlands) (Table S2).³ Most pools were embedded in landscapes of low LUI, as the average size of forest blocks surrounding study pools was 289 ha (range 13–742 ha) and was characterized by median LUI values of 1.1 (150 m; continuous forest) and 1.9 (500 m; open woodlands). LUI within 150 m of pools was significantly less than at 500 m ($t_{[86]} = -1.856$, p = 0.033). The study area was characterized by high wetland density

Table 1. Model selection for wood frog (*Rana sylvatica*) breeding pool and landscape (150 and 500 m scales) habitat associations with breeding population size (reproductive effort).

Model	AIC _c	ΔAIC_c	Weighted Akaike w _i	Evidence ratio
Hydroperiod ⁽⁺⁾ + density potential breeding pools 500 m scale ⁽⁻⁾	392.654	0	0.218	1.000
Hydroperiod ⁽⁺⁾ + density potential breeding pools 150 m scale ⁽⁻⁾	393.362	0.708	0.153	1.425
Hydroperiod ⁽⁺⁾ + area other wetlands 150 m scale ⁽⁻⁾	393.369	0.715	0.153	1.430
Hydroperiod ⁽⁺⁾ + area other wetlands 500 m scale ⁽⁻⁾	393.888	1.234	0.118	1.853
Hydroperiod ⁽⁺⁾	394.180	1.526	0.102	2.145
Hydroperiod ⁽⁺⁾ + land-use intensity (LUI) at 150 m scale ⁽⁺⁾	395.669	3.015	0.048	4.515
Hydroperiod ⁽⁺⁾ + pool canopy openness ⁽⁺⁾	395.919	3.265	0.043	5.117
Hydroperiod ⁽⁺⁾ + forest composition ⁽⁺⁾	395.921	3.267	0.043	5.122
Hydroperiod ⁽⁺⁾ + forest structure ⁽⁺⁾	395.994	3.340	0.041	5.312
Hydroperiod ⁽⁺⁾ + LUI at 500 m scale ⁽⁺⁾	396.450	3.796	0.033	6.673
Area other wetlands 150 m scale ⁽⁻⁾	398.933	6.279	0.009	23.092
Density potential breeding pools 150 m scale ⁽⁻⁾	399.074	6.420	0.009	24.779
Density potential breeding pools 500 m scale ⁽⁻⁾	399.586	6.932	0.007	32.008
Area other wetlands 500 m scale ⁽⁻⁾	400.363	7.709	0.005	47.205
Forest composition ⁽⁺⁾	400.380	7.726	0.005	47.608
Forest structure ⁽⁺⁾	400.924	8.270	0.003	62.490
LUI at 150 m scale ⁽⁺⁾	401.193	8.539	0.003	71.486
Pool canopy openness ⁽⁺⁾	401.229	8.575	0.003	72.784
LUI at 500 m scale ⁽⁺⁾	401.522	8.868	0.003	84.268
All variables	401.532	8.878	0.003	84.690

Note: Candidate models (20 in total) nearer the top of the table are more closely associated with greater wood frog breeding populations (eggmass counts). Those with evidence ratio <3 (i.e., first five models in the table) are selected. Positive coefficient values for a given variable in the model are indicated with a ⁽⁺⁾ and negative with a ⁽⁻⁾. AIC_c values are means generated for each model from 30 iterations of negative binomial regression.

(~9% of the landscape or 1.77 breeding pools/km²), with the result that no breeding pool was completely isolated from other wetlands at either spatial scale (Table S2).³

Model selection results

Model selection informed by AIC suggests that poolbreeding wood frog populations are positively associated with geographically isolated, longer hydroperiod seasonal pools (Table 1). The selected set of candidate models (74.4% of total model weight for all candidate models) comprised models with longer hydroperiod and fewer neighboring wetlands. Hydroperiod was the most influential variable, included in all models in the confidence set (95% of total weight), and was the only single-parameter model in the top-ranking selected set. Forest structure and composition, pool canopy openness, and LUI (all positive slopes) were not present in influential models (8.4%, 4.3%, and 4.8% of the total weight, respectively).

Spotted salamanders showed a similar pattern to that of wood frogs (Table 2), with longer pool hydroperiod and relative isolation positively associated with local breeding populations. Of additional significance to spotted salamanders was forest composition (PC2), with larger breeding populations associated with increased forest maturity. Specifically, seasonal pools embedded in stands dominated by late-successional tree species hosted greater breeding effort by spotted salamanders. Omitting pools with hydroperiods less than 16 weeks from the spotted salamander analysis did not alter the results of model selection.

Because all models in the AIC selected set are similar in weight, it seems that (i) longer hydroperiod seasonal pools

in combination with (*ii*) a degree of pool isolation (<13 breeding pools and 15 ha of forested wetland within 150 m, and <19 breeding pools and 40 ha of forested wetland within 500 m) and (*iii*) local forest maturity indicators (spotted salamanders only) yielded the greatest influence on pool-breeding amphibian populations in this study.

The importance of hydroperiod alone was further supported by goodness-of-fit testing of the distribution of wood frog and spotted salamander egg masses among discrete pool inundation classes (Table 3). Long hydroperiod pools (\geq 18 weeks in duration) accounted for only half of all pools studied, yet hosted nearly 75% of all egg masses deposited by either species (Fig. 2, Table 3). For both species, local breeding population size increased markedly, and similarly, along a hydroperiod gradient from 9 to 29 weeks (Fig. 2).

Fifteen pools (17.2% of all pools) showed signs of having once been borrow pits, farm ponds, or otherwise created or modified pools, subsequently naturalized during post-agricultural abandonment and reforestation. Compared with natural pools (median 17 weeks, range 20 weeks), anthropogenic pools had significantly longer hydroperiods (median 20.5 weeks, range 9 weeks; Mann-Whitney U test, U = 807). The distribution of breeding effort by wood frogs and spotted salamanders at naturalized pools (24.3% of egg masses) was not significantly different from expected given their frequency of occurrence (17.2%). Furthermore, among long hydroperiod pools alone (≥ 18 weeks, N = 43), there was no significant difference in number of egg masses between pools of natural (N = 32 pools; 158.6 ± 146.2) versus anthropogenic origin or modification (N = 11; 188.3 \pm 196.0; Mann–Whitney U test, U = 162).

Table 2. Model selection for spotted salamander (*Ambystoma maculatum*) breeding pool and landscape (150 and 500 m scales) habitat associations with breeding population size (reproductive effort).

Model	AIC _c	ΔAIC_{c}	Weight Akaike w _i	Evidence ratio
Hydroperiod ⁽⁺⁾ + area other wetlands 150 m scale ⁽⁻⁾	360.397	0.000	0.302	1.000
Hydroperiod ⁽⁺⁾ + area other wetlands 500 m scale ⁽⁻⁾	360.889	0.493	0.236	1.279
Hydroperiod ⁽⁺⁾ + forest composition ⁽⁺⁾	361.352	0.956	0.187	1.613
Hydroperiod ⁽⁺⁾ + density potential breeding pools 500 m scale ⁽⁻⁾	361.596	1.199	0.166	1.821
Hydroperiod ⁽⁺⁾ + density potential breeding pools 150 m scale ⁽⁻⁾	364.704	4.308	0.035	8.619
Hydroperiod ⁽⁺⁾	365.315	4.919	0.026	11.698
Hydroperiod ⁽⁺⁾ + pool canopy openness ⁽⁺⁾	366.726	6.329	0.013	23.680
Hydroperiod ⁽⁺⁾ + LUI at 150 m scale ⁽⁺⁾	367.092	6.696	0.011	28.443
Hydroperiod ⁽⁺⁾ + LUI at 500 m scale ⁽⁺⁾	367.448	7.052	0.009	33.984
$Hydroperiod^{(+)} + forest structure^{(+)}$	368.044	7.647	0.007	45.775
Forest composition ⁽⁺⁾	369.055	8.658	0.004	75.872
Area other wetlands 500 m scale ⁽⁻⁾	371.280	10.883	0.001	230.821
Area other wetlands 150 m scale ⁽⁻⁾	371.465	11.069	0.002	253.241
All variables	372.229	11.832	0.001	370.931
Density potential breeding pools 150 m scale ⁽⁻⁾	373.478	13.081	0.000	692.662
Density potential breeding pools 500 m scale ⁽⁻⁾	374.363	13.967	0.000	1078.517
Forest structure ⁽⁺⁾	376.169	15.772	0.000	2660.251
Pool canopy openness ⁽⁺⁾	376.186	15.789	0.000	2682.960
LUI at 150 m scale ⁽⁺⁾	376.796	16.400	0.000	3640.741
LUI at 500 m scale ⁽⁺⁾	376.853	16.456	0.000	3744.871

Note: Candidate models (20 in total) nearer the top of the table are more closely associated with greater spotted salamander breeding populations (egg-mass counts). Those with evidence ratio <3 (i.e., first four models in the table) are selected. Positive coefficient values for a given variable in the model are indicated with a ⁽⁺⁾ and negative with a ⁽⁻⁾. AIC_c values are means generated for each model from 30 iterations of negative binomial regression.

Discussion

Breeding population assessment

We used reproductive effort as a relative indicator of breeding population size and consequently pool and terrestrial habitat quality given that estimates of egg mass per adult are known (e.g, wood frog - 1 mass/female annually (Crouch and Paton 2000); spotted salamander - 2-4 masses/female per 1-3 years (Windmiller 1996; Petranka 1998)). Because pool-breeding amphibians tend to be philopatric (Berven and Grudzien 1990; Petranka 1998), repeated successful individual choices of breeding pool are likely to result in higher population-level reproductive effort than in pools where breeding habitat quality is low or terrestrial habitat constrains the return of breeding adults. For these reasons, our results showing that both wood frogs and spotted salamanders had higher breeding populations in longer hydroperiod pools (18 weeks) have significant implications for conservation of pool-breeding amphibians. Although egg-mass counts (reproductive effort) are not a direct measure of reproductive success, we suggest that they are a useful metric for assessing the quality of the pool (Resetarits 1996) and its adjacent terrestrial habitat.

The occupancy rates we observed for breeding pools by wood frogs and spotted salamanders are higher (80%–90%) than previously reported for either species. Calhoun et al. (2003) reported 70.4% occupancy by spotted salamanders and 40% occupancy by wood frogs for 155 pools throughout Maine. Egan and Paton (2004) reported 69% occupancy rates by both species at 124 ponds in Rhode Island and Babbitt et al. (2003) reported that 48% of 42 wetlands surveyed had evidence of wood frog reproduction in New Hampshire, whereas Windmiller (1996) observed spotted salamanders

breeding in 49% of 193 wetlands surveyed in eastern Massachusetts. The exceptional occupancy rates of our wetlands by pool-breeding species is likely a result, in part, of our selection of plausible breeding wetlands for these species i.e., forested pools of only temporary or semi-permanent (i.e., seasonal hydroperiod). We are supported in this conclusion by a similar study from Rhode Island in which wood frogs and spotted salamanders were found in 64%– 81% and 59%–76%, respectively, of seasonal pools (N =61) over a 5-year study (Skidds and Golet 2005). Focusing on a narrower set of pools for habitat suitability studies, as we did, may provide a finer degree of information on which hydroperiods are most suitable for seasonal pool-breeding species.

Hydroperiod and relative pool isolation

Much work has been done on pool-breeding amphibians linking hydroperiod to species composition (Snodgrass et al. 2000; Babbitt et al. 2003; Babbitt 2004) and larval growth and development (Newman 1992, Skelly 1996). For example, increasing hydroperiod tends to produce more complex inter- and intra-specific larval competition and predation (Wilbur 1972, Wellborn et al. 1996, Altwegg 2002), with effects on growth and development (Rowe and Dunson 1995) and larval survival (Pechmann et al. 1989). Our observations on the strong link between hydroperiod and reproductive effort suggest that the population of adult pool-breeding amphibians are also strongly influenced by hydroperiod. This linkage is clearer because we were working in relatively unfragmented systems where quality of terrestrial habitat was not an issue driving study-site selection. Both species were more abundant in pools that held water through mid-

Wood fr	Wood frog		Spotted salamander	
e of pools in Observe od category masses	χ^2	Observed masses	χ^2	
94	8.7(-)	43	24.4(-)	
116	548.9(-)	62	422.0(-)	
1239	234.7(-)	719	292.9 ⁽⁻⁾	
4082	666.7(+)	3081	$687.8^{(+)}$	
))	e of pools in d category 94 116 1239 4082	$ \begin{array}{c} \hline Wood \ frog \\ \hline Observed \\ masses & \chi^2 \\ \hline 94 & 8.7^{(-)} \\ 116 & 548.9^{(-)} \\ 1239 & 234.7^{(-)} \\ 4082 & 666.7^{(+)} \\ \end{array} $	$ \begin{array}{c c} \hline Wood \ frog \\ \hline Observed \\ masses \\ \hline \chi^2 \\ \hline \\ 94 \\ 116 \\ 548.9^{(-)} \\ 1239 \\ 4082 \\ \hline \\ 4082 \\ \hline \\ 666.7^{(+)} \\ \hline \\ 3081 \\ \hline \\ \hline \\ \hline \\ \hline \\ \\ \hline \\ \hline \\ \\ \hline \\ \hline \hline \\ \hline \\ \hline \hline \hline \hline \\ \hline \hline \hline \hline \\ \hline \hline \hline \hline \hline \hline \hline \\ \hline \hline$	

 Table 3. Observed versus expected use of ecologically relevant seasonal hydroperiod categories by vernal pool-breeding amphibian species in southern Maine, USA.

Note: An α (0.0125) for multiple comparisons was used and all χ^2 comparisons were statistically significant. Whether more (+) or less (–) egg masses were observed than expected is indicated for each hydroperiod category.

Fig. 2. Hydroperiod and breeding population (reproductive effort) relationships for two vernal pool-breeding amphibians (wood frog, *Rana sylvatica*, and spotted salamander, *Ambystoma maculatum*) in southern Maine, USA, in 2002 and 2003. Vertical broken lines indicate hydroperiod categories of <12.5, 12.5–15, 16–17, and ≥18 weeks after the onset of breeding (early April in the study area), corresponding with developmental periods (see Materials and methods). Values within hydroperiod categories in the top two panels indicate the percentage of egg masses that occur within each hydroperiod category. In the lowest panel, percentages that are underlined indicate the percentage of pools (n = 87) in each hydroperiod category.



summer, potentially the driest period in northeastern seasonal pools (Fig. 2, Table 3). These longer hydroperiod pools likely provide a "safe", intermediate inundation period, permitting pool-breeding amphibians to hedge against the deleterious effects of drought within a relatively lowdensity predator environment (Wilbur 1972; Wellborn et al. 1996; Kolozsvary 2003; Relyea 2004). Longer hydroperiod seasonal pools permit longer larval periods that may have adaptive value to local populations by influencing such fitness traits as size at metamorphosis, age of reproduction, and survival to first reproduction (Rowe and Ludwig 1991; reviewed by Paton and Crouch 2002; Altwegg and Reyer 2003).

Previous studies of hydroperiod-biota relationships have generally included a broader continuum of water regimes, from temporary to permanent. Babbitt et al. (2003) found that the shortest hydroperiod wetlands measured (<16 weeks) were dominated by wood frogs (a species with fast developmental periods), whereas intermediate hydroperiod wetlands (\geq 16 weeks but less than permanent) contained the greatest abundance of both wood frogs and spotted salamanders. Our observations are complementary to Babbitt et al. (2003) in that those pools receiving greatest use (\geq 18 weeks in hydroperiod) were analogous to their "intermediate" pools. The significant hydroperiod influence that we observed is independent of the effects of elevated populations of predatory fish and invertebrates associated with permanent ponds (Wellborn et al. 1996; Colburn 2004).

The proximity of neighboring suitable breeding wetlands as potential source populations is generally considered a favorable landscape attribute that contributes to regional population viability (Gill 1978; Gibbs 1993; Trenham et al. 2003; Petranka et al. 2004). Although clusters of breeding pools within dispersal distance of one another contribute to larger regional population sizes of mobile pool-breeding species, individual pools within a cluster may host smaller populations than equivalent pools in an isolated context (Petranka et al. 2004). Similarly, our habitat modeling results for wood frogs and spotted salamanders suggest that a degree of isolation from alternative breeding sites can contribute to locally elevated breeding populations. Such partially isolated pools may attract disproportionate use by virtue of having fewer satellite pools as choices (Calhoun et al. 2003). We suggest that the identification of partially isolated, high-use pools is an important complement to traditional conservation approaches for pool-breeding amphibians that emphasize the value of protecting highly visible wetland clusters. Gibbs (1993, 1998) has illustrated the importance of wetland number and spatial distribution (in addition to area) as a metric for assessing the ecological integrity of landscapes. These relatively isolated wetlands play a stepping-stone function in reducing interwetland distances and will be increasingly important in urbanizing landscapes where interwetland distances increase (Gibbs 2000; Rubbo and Kiesecker 2005).

Forest extent and maturity

Declines in pool-breeding amphibian populations have been previously documented in landscapes undergoing high rates of land-use conversion and fragmentation (Kolozsvary and Swihart 1999; Lehtinen et al. 1999; Waldick et al. 1999; Guerry and Hunter 2002), with specific impacts observed in both wood frogs and spotted salamanders (Homan et al. 2004; Porej et al. 2004; Herrmann et al. 2005; Rubbo and Kiesecker 2005). Our study area has not been intensively harvested for decades; however, while portions are becoming urbanized (Plantinga et al. 1999), most have likely not passed critical thresholds of forest cover loss detectable by our breeding populations (i.e., Herrmann et al. 2005). In our study, focusing research in this urbanizing region helped us to identify local, fine-scale environmental correlates of breeding success in a relatively intact landscape that may, in turn, be applied to active conservation in more rapidly developing forested landscapes.

Later successional forests provide several structural characteristics selected by spotted salamanders during the postbreeding phase of their life history (Madison 1997; deMaynadier and Hunter 1998, 1999; Faccio 2003). Our results are the first to suggest that breeding population size of spotted salamanders may similarly be affected by the availability of mature forest structure — specifically, dominance by longlived, shade-tolerant overstory trees. In our landscape, forest maturity was closely related to whether or not areas were burned in the catastrophic fire of 1947 that largely denuded areas of existing vegetation and organic soil (Butler 1987). Spotted salamanders are fossorial (Petranka 1998), generally selecting areas of deep forest litter and organic material, abundant rotting wood, and leaf-covered small-mammal runways and tunnels (Windmiller 1996; Madison 1997; Faccio 2003; Regosin et al. 2003b) — elements that have yet to recover from the effects of severe fire in southern Maine. Specific forest structural preferences by wood frogs are not as well documented, but forest anurans generally may be less specialized than salamanders for elements of forest microhabitat that preserve cool, moist conditions (Heatwole 1961; Bellis 1962; Baldwin 2005). Compared with salamanders, anurans generally have greater dispersal capability (Semlitsch and Bodie 2003), higher operating and tolerance temperatures (Stebbins and Cohen 1995), and a greater capacity for bladder water storage (up to 20%-30% of their body mass; Zug 1993), which may partly explain their apparent tolerance for warmer and drier conditions (deMaynadier and Hunter 1995). Rather, the overall extent of contiguous forest habitat (Homan et al. 2004; Porej et al. 2004; Rubbo and Kiesecker 2005) and proximity of post-breeding forested wetlands (for summer foraging and estivation; Baldwin 2005) may be the most important factors affecting local wood frog populations.

Conservation implications

Researchers have recommended that a broad spectrum of hydroperiods, from seasonal to permanent, be conserved at regional scales to provide a diversity of habitat for wetlandbreeding amphibians (Snodgrass et al. 2000; Babbitt et al. 2003) and invertebrates (Colburn 2004). We suggest that for many pool-obligate amphibians of northeastern North America the optimal breeding habitat is long-hydroperiod seasonal pools. In particular, we recommend that seasonal pools containing water for greater than 16-17 weeks postbreeding onset be recognized by managers as key breeding habitat for wood frogs and spotted salamanders (see also Paton and Crouch 2002). These longer hydroperiod seasonal pools (49% of all pools in our study) may provide valuable source populations that are capable of buffering regional population dynamics, especially during periods of drought. Surrogates for predicting hydroperiod may be useful in some regions (see Mitchell 2005; Skidds and Golet 2005). Furthermore, relative pool isolation in our study also contributed to greater breeding effort, highlighting the potential significance of conserving high-value, stepping-stone pools that lie outside of, but potentially link, high-visibility wetland clusters.

Finally, we recognize the value of a historical perspective on ecosystem development for conservation planning generally (Foster 2000) and for pool-breeding amphibians specifically in reforested, developing landscapes. Nearly 20% of the seasonal pools in this study were reforested, modified pools. These long-hydroperiod seasonal pools supported comparable levels of breeding amphibians with that of

"natural" long-hydroperiod seasonal pools. The supplemental value of anthropogenic breeding pools is especially relevant in landscapes undergoing a high rate of wetland loss and degradation, such as in northeastern North America (Dahl 2000). Throughout this region, older farm ponds, gravel pits, and cellar holes are common and, following abandonment and succession, often provide the critical attributes of high-value seasonal pools, which include fishlessness, long hydroperiod, and a largely (re)forested life zone. By extension, recently created pools that today seem unsuitable as conservation targets (e.g., borrow pits, agricultural ponds) may eventually become reforested and serve as valuable breeding sites. Our results lend further support for an increased recognition of the potential significance of anthropogenic pools to the conservation of pool-breeding amphibians in fragmented landscapes.

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