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The relative importance of wetland size and hydroperiod for amphibians in southern New Hampshire, USA

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Abstract

In the United States, the regulatory approach to wetland protection has a traditional focus on size as a primary criterion, with large wetlands gaining significantly more protection. Small, isolated wetlands have received less protection; however, these wetlands play a significant role in the maintenance of biodiversity of many taxonomic groups, including amphibians. An important question for directing conservation and management efforts for amphibians is whether size is a useful criterion for regulatory decisions. Because hydroperiod has an important influence on amphibian composition in wetlands, I conducted a study to examine the relative influence of wetland size and hydroperiod on amphibian occurrence. I sampled 103 wetlands in southern New Hampshire in 1998 and 1999 using dipnet sampling to document the presence of larval amphibians. Wetlands were placed into one of three hydroperiod categories; short (<4 months), intermediate (4–11 months), or long (permanent) based on field observations of drying pattern. Wetland size was determined from digitized national wetland inventory (NWI) maps (most wetlands) or measured in the field. I examined patterns of amphibian species richness and individual species occurrence using generalized linear models. Wetland size ranged from 0.01 to 3.27 ha. Overall, species richness was significantly influenced by hydroperiod ($\chi^2 = 18.6$, $p < 0.001$), but not size ($\chi^2 = 1.4$, $p = 0.24$). Examination within hydroperiod categories revealed several significant relationships with wetland size. Species richness was related to wetland size in wetlands with short and intermediate hydroperiods, but not wetlands with long hydroperiods. Wetland size does not appear to be a useful sole criterion for determining wetland functional value for amphibians; assessments of functions of seasonally inundated wetlands for amphibians would benefit from examination of hydroperiod.

Introduction

Wetland size has been used as one of the primary criteria for assigning protected status to wetlands in the United States, with greater protection given to larger wetlands. Increased understanding of the function served by small wetlands (Moler and Franz 1987; Semlitsch and Bodie 1998) has led to concern that size may not be a suitable criterion upon which to make regulatory decisions. For certain species, small isolated wetlands are critical habitats, and species strongly associated with these

wetlands may not persist in landscapes in which the loss of these wetlands is significant. Where small wetlands are common in the landscape, loss of wetlands below existing protection size classes would result in increased distances between wetlands, potentially disrupting dispersal and consequent rescue necessary for functioning metapopulations (Gibbs 1993, 2000; Semlitsch and Bodie 1998).

A key process in small isolated wetlands is the seasonal or semi-annual drying regimes that preclude establishment of populations of predatory fish. Many species of amphibians breed extensively or exclusively in these small isolated wetlands, and the larvae of these species cannot persist with fish predators. The negative impacts of fish on these species are so significant that the adults of many amphibian species avoid breeding in water bodies with predatory fish (Hopey and Petranka 1994; Binckley and Resitarits 2003). To assess the ecological function of both small and large wetlands, it is necessary to determine how wetland size is related to amphibian use.

Because wetland size could be a simple criterion for wetland valuation, it is important to determine if it is also a functionally useful criterion. If amphibians distribute predictably along a gradient of wetland size (e.g., higher species richness in larger wetlands), this variable could be an efficient metric for guiding wetland regulations. However, if wetland size is a poor predictor of amphibian species occurrence, then regulations based on size will probably not provide adequate means for protecting amphibian populations or for predicting the true impacts of wetland loss. In conducting this study, I considered several pertinent questions. First, is there a consistent relationship between size and hydrology (i.e., do larger wetlands have longer hydroperiods)? Second, is amphibian species richness related more strongly to wetland size or to hydroperiod? If the answer is hydroperiod, then only a strong relationship between hydroperiod and wetland size would allow size to be a useful functional criterion for management of amphibian populations. Third, are there potential differences in the relationship between size, hydroperiod, and species richness when comparing amphibian use along the gradient from small to large wetlands? For example, among wetlands with short hydroperiods, do small or large wetlands have high species richness?

Methods

Study area

Research was conducted across a 4800 km^2 area of southern and central New Hampshire. The study area is predominantly forested (i.e., rural), with scattered agriculture and urban/suburban development. Forest cover type in the study area is predominantly secondary growth (> 50 years) oak/pine forest. Dominant tree species included white pine (*Pinus strobes* L.), red maple (*Acer rubrum* L.), red oak (*Quercus rubra* L.), and eastern hemlock (*Tsuga canadensis* L.). A majority of wetland study sites (n = 61) were selected randomly through a selection of 'blocks' created from universal transverse mercator (UTM) grid lines on US Geological Survey 7.5 min topographic map. Random pairs of coordinates were chosen to determine which UTM blocks would be used. I used national wetlands inventory (NWI) maps and field surveys to locate study wetlands and to verify wetland classification within each UTM block. All wetlands considered suitable were palustrine scrub–shrub, emergent, or forested, and were chosen to represent the hydrological gradient from very temporary to permanent. Over 150 wetlands were initially field checked. Many wetlands were located on private property; therefore, wetlands on lands for which I could not obtain permission were rejected from the study. In addition, I rejected farm ponds or other constructed wetlands. Within each of 61 UTM blocks, the first suitable wetland for which I could obtain landowner permission for sampling was selected. I also sampled wetlands (n = 42) on a variety of public lands. In this case I first located wetlands with long hydroperiods that were accessible (i.e., within a kilometer of a trail) using NWI maps, and then selected additional sites for sampling that were non-permanent.

I sampled each wetland twice annually between May–September in 1998 and 1999. The first sampling period was conducted during May and June, and the second sample period was from July through early September. The timing of sampling allowed me to determine occurrence of early (spring) and late (summer) breeding species.

Each wetland was divided into microhabitats based on combinations of depth (greater or less than 0.6 m deep) and the presence or absence of

submersed and/or emergent vegetation. Sampling effort was dispersed equally among the microhabitats present within each wetland using replicate 1 m^2 sweeps with a 30×45 cm dipnet. The number of sweeps varied with wetland size and the number of microhabitats present, and ranged from five in very small wetlands with little microhabitat variation to 60 sweeps in large wetlands. Using a larger number of sweeps in larger wetlands enabled me to sample throughout a greater area of the wetland, and thus reduce the risk of missing species that may have been concentrated in one area. In addition, sampling portions of all microhabitats ensured capture of any species that may be associated with a specific microhabitat. The size of many wetlands and the number of wetlands sampled precluded efficient use of a grid system for random sampling, so haphazard sampling was used, in which sweeps were spread throughout the microhabitats. Examination of sampling data indicated that no new species were added at any wetland during the second year of sampling, suggesting that sampling efforts were sufficient at capturing all species.

All amphibian larvae captured that could not be accurately identified to species in the field were preserved in 10% buffered formalin and identified to species using standard keys (Orton 1939; Altig 1970; Travis 1981). Occurrence of each species based on captures of larvae, as well as species richness, was determined for each wetland.

Wetland area was computed using a Geographic Information System (ArcInfo; ESRI 1999) with the exception that small wetlands (n = 10) not included on digitized NWI maps were measured in the field with a meter tape in June 1998, which corresponded to approximate high water level that year. I placed wetlands in one of three hydroperiod classes based on assessment at all wetlands during sampling and monthly field visits in October and November for a subset of wetlands (to differentiate intermediate versus long hydroperiods). Wetlands were classified as having short hydroperiods if they were inundated for <4 months after ice out (drying prior to July in both years). Wetlands were characterized as having intermediate hydroperiods if they dried after July 1 (>4 months, but <12 months) or in a few cases if they dried in one of the two years (i.e., semi-annual drying). Finally, wetlands that never dried during the study were classified as long.

Statistical analyses

I performed a Spearman's rank correlation to determine the extent to which hydroperiod and wetland size were correlated. An ANOVA with posthoc Tukey's pairwise comparisons was used to determine if wetland size or amphibian species richness differed among the three hydroperiod categories.

I used generalized linear models (McCullagh and Nelder 1989) to determine the relative influence of wetland size and hydroperiod on amphibian species richness and species occurrence. I also examined the influence of wetland size on amphibian species richness and species occurrence with each hydroperiod category. Generalized linear models present a major advantage over classical multiple regression approaches in that they integrate data from different statistical distributions with the appropriate modeling of statistical error (e.g., normal as in multiple regression, binomial for occurrence data, ordinal for classes of abundance, Poisson or negative binomial for species or individual counts). Amphibian species richness was analyzed using a normal response distribution with a canonical-link function, and occurrence of each species was analyzed using a binomial regression with a logit-link function (McCullagh and Nelder 1989). I tested model deviance (explained variance) using χ^2 tests (McCullagh and Nelder 1989). Where necessary, data were transformed to improve normality. Statistical procedures were analyzed using SAS (Version 8, 2001).

Results

Wetlands sampled ranged in size from 0.01 to 3.27 ha. Wetland size and hydroperiod were correlated (r_s = 0.56). Wetland size differed significantly among hydroperiod categories ($F_{2,\ 100}$ = 13.417, $p < 0.001$; Figure 1); wetlands with short hydroperiods were significantly smaller than wetlands with intermediate (p = 0.031) and long ($p < 0.001$) hydroperiods, and wetlands with intermediate hydroperiods were smaller than wetlands with long hydroperiods (p = 0.006).

I collected 19,702 individual larvae of 9 species from 103 wetlands. Amphibian species richness was influenced significantly by hydroperiod

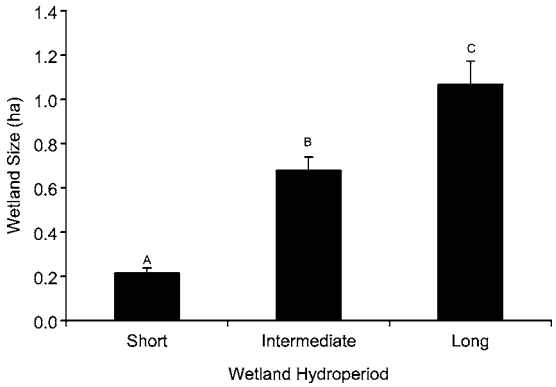


Figure 1. Comparison of wetland size for wetlands with short (inundated <4 months), intermediate (inundated >4 months, nonpermanent), and long (permanent) hydroperiods. Bars are mean + 1 SE. Bars with different letter are statistically different.

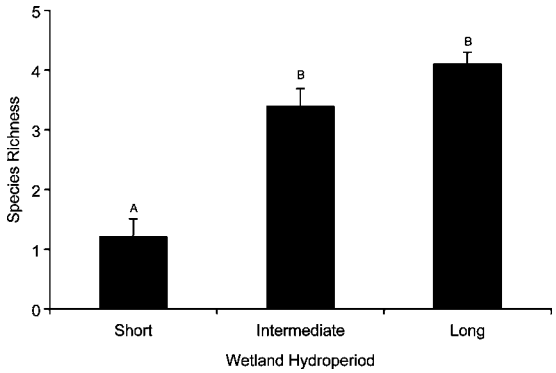


Figure 2. Amphibian species richness in wetlands with short (inundated <4 months), intermediate (inundated >4 months, nonpermanent), and long (permanent) hydroperiods. Bars are mean + 1 SE. Bars with different letter are statistically different.

($F_{2,100}$ = 17.41, p < 0.001; Figure 2). Species richness was higher in wetlands with intermediate (p < 0.001) and long hydroperiods (p < 0.001) compared to wetlands with short hydroperiods; species richness in wetlands with intermediate and long hydroperiods did not differ significantly (p = 0.102).

General linear models indicted that, across the entire data set of 103 wetlands, hydroperiod had a significant effect on both species richness and occurrence patterns of individual species, but wetland size did not (Table 1). Green frog (*Rana clamitans* Latreille) was the only species for which wetland size had a significant influence on presence (Table 1).

A more refined picture of the relationship between wetland size and hydroperiod and the influence of these factors on amphibian patterns of occurrence was revealed by examining patterns within each wetland hydroperiod category

Table 1. The relationship between amphibian species richness and species occurrence and independent variables (wetland size and hydroperiod) based on generalized linear models. Model deviance represents % variance in species richness explained by the model.

Dependent variable	Independent variable	Model deviance (%)	χ^2	p
Species richness	Hydroperiod	23.8	18.6	<0.001
	Wetland size		1.4	0.240
Rana catesbeiana	Hydroperiod	21.3	9.4	0.002
	Wetland size		0.8	0.36
Rana clamitans	Hydroperiod	45.1	18.2	<0.001
	Wetland size		6.0	0.014
Rana sylvatica	Hydroperiod	19.0	14.0	<0.001
	Wetland size		1.0	0.313
Rana palustris	Hydroperiod	26.8	17.6	<0.001
Bufo americanus	Hydroperiod	8.7	3.2	0.075
	Wetland size		0.1	0.734
Pseudacris crucifer	Hydroperiod	7.1	4.1	0.043
	Wetland size		1.2	0.277
Hyla versicolor	Hydroperiod	7.0	5.6	0.018
	Wetland size		0.2	0.618
Notophthalmus viridescens	Hydroperiod	15.9	9.1	0.003
	Wetland size		2.2	0.141
Ambystoma maculatum	Hydroperiod	1.6	0.6	0.439
	Wetland size	2.6	2.6	0.106

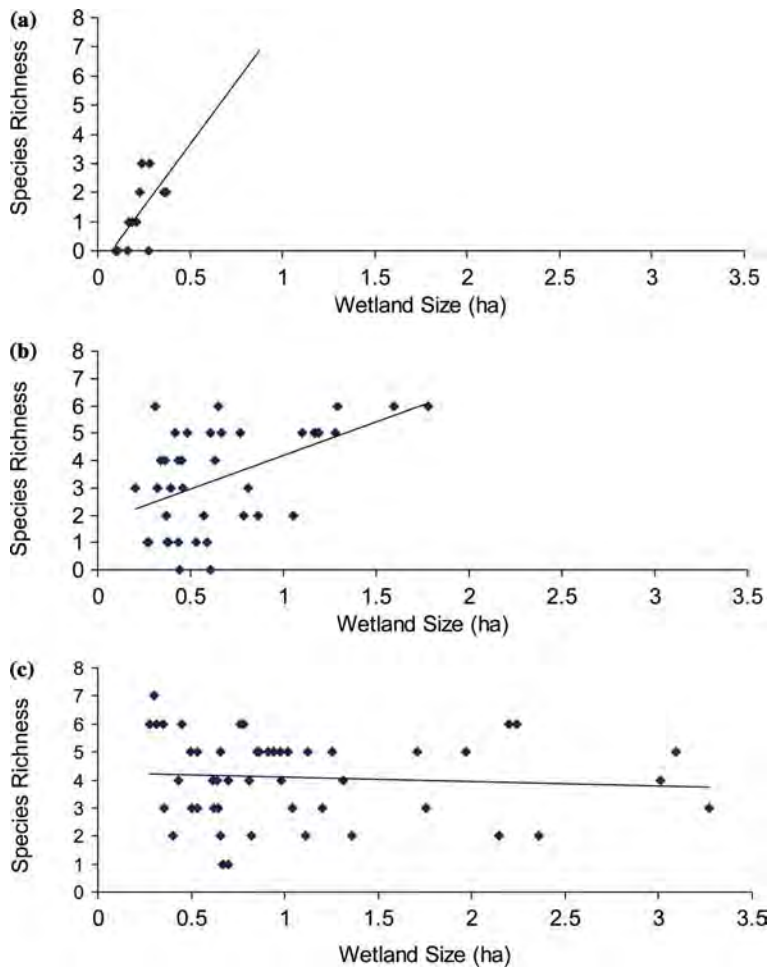


Figure 3. Relationship between wetland size and amphibian species richness in (a) wetlands with short (inundated < 4 months; $n = 14$); (b) intermediate (inundated > 4 months, nonpermanent; $n = 39$); and (c) long (permanent; $n = 50$) hydroperiods. Lines are best fit; refer to Table 1 for statistical testing based on generalized linear models.

(Figure 3). Wetland size had a significant effect, and explained 32.2% of the variation in species richness patterns in wetlands with short hydroperiods, and 19.3% in wetlands with intermediate hydroperiods (Table 2). In contrast, wetland size did not have a significant effect on species richness in wetlands with long hydroperiods (Table 2).

Among species breeding in wetlands with short hydroperiods, the wood frog (*Rana sylvatica* LeConte) was significantly influenced by wetland size and occurred most frequently in the smallest wetland size class (< 0.25 ha) (Figure 4). Among wetlands with intermediate hydroperiods, wetland size had the most significant effect on occurrence patterns of *R. clamitans*, which was more likely to be found in larger wetlands (Figure 4). The spring peeper (*Pseudacris crucifer* Wied-Neuwied) also was significantly influenced by wetland size, and the gray treefrog (*Hyla versicolor* Cope) and the red-spotted newt (*Notophthalumus viridescens* Rafinesque) were marginally influenced by wetland size. However, the patterns of occurrence among these species do not show strong directionality (i.e., tendency for use of smaller or larger wetlands), and generally explained less than 15% of the variation in occurrence within intermediate wetlands (Table 2, Figure 4). The American toad (*Bufo americanus* Holbrook) occurred only in the largest size class of wetlands with intermediate hydroperiods (Figure 4). Only one species, the spotted salamander (*Ambystoma maculatum* Shaw), was significantly influenced by wetland size

Table 2. The relationship between species richness and species occurrence with wetland size in short (<4 month hydroperiod), intermediate (wetlands with hydroperiods >4 months or drying one of two years), and long (permanent) hydroperiod wetlands based on generalized linear models. Model deviance represents % variance in species richness explained by the model.

Dependent variable	Independent variable	Model deviance (%)	χ^2	*p*
Short hydroperiod wetlands				
Species richness	Wetland size	32.2	5.6	0.018
Rana sylvatica	Wetland size	30.7	5.0	0.025
Pseudacris crucifer	Wetland size	4.5	0.6	0.482
Ambystoma maculatum	Wetland size	21.1	3.1	0.078
Intermediate hydroperiod wetlands				
Species Richness	Wetland size	19.3	9.5	0.002
Ambystoma maculatum	Wetland size	0.5	0.2	0.618
Bufo americanus	Wetland size	23.3	2.7	0.099
Hyla versicolor	Wetland size	13.6	5.6	0.053
Notophthalmus viridescens	Wetland size	8.3	3.7	0.053
Pseudacris crucifer	Wetland size	10.3	4.1	0.042
Rana catesbeiana	Wetland size	0	0.4	0.527
Rana clamitans	Wetland size	30.5	8.5	0.004
Rana palustris	Wetland size	0	0.1	0.837
Rana sylvatica	Wetland size	6.4	2.3	0.120
Long hydroperiod wetlands				
Species Richness	Wetland size	0.6	0.3	0.581
Ambystoma maculatum	Wetland size	9.0	4.2	0.041
Bufo americanus	Wetland size	0	0	0.849
Hyla versicolor	Wetland size	0.3	0.4	0.526
Notophthalmus viridescens	Wetland size	0.5	0.3	0.611
Pseudacris crucifer	Wetland size	0	0	0.954
Rana catesbeiana	Wetland size	0.4	0.5	0.459
Rana clamitans	Wetland size	0	0.2	0.696
iRana palustris	Wetland size	4.0	2.1	0.147
Rana sylvatica	Wetland size	1.8	0.4	0.358

among wetlands with long hydroperiods; *A. maculatum* was less likely to be found in the largest wetlands (Table 2, Figure 4).

Discussion

Several researchers have recently called into question the suitability of using wetland size as a criterion for assessing wetland function (Semlitsch and Bodie 1998; Snodgrass et al. 2000; Paton and Crouch 2002; Babbitt et al. 2003). The results of this study indicate that wetland hydroperiod has a stronger influence than wetland size on both amphibian species richness and the presence/absence of amphibian species. Of the nine amphibians species documented in the 103 wetlands in this study, none was more strongly influenced by wetland size than hydroperiod.

The important influence that wetland hydroperiod has on habitat suitability for amphibians is widely recognized (Wellborn et al. 1996; Semlitsch 2000). Differences in life history and behavioral traits result in species-specific patterns of distribution that are largely driven by the amount of time a breeding site holds water and ability to persist with predators, particularly fish (Woodward 1983; Skelly 1996). Because predator composition and abundance at a wetland site is also influenced by hydroperiod, it is not surprising that wetland hydroperiod should be such an important factor influencing amphibian distribution patterns. Amphibian species are not distributed randomly relative to hydroperiod, but rather show patterns of turnover across the hydrological gradient (Snodgrass et al. 2000; Babbitt et al. 2003). Thus, only by maintaining wetlands with a diversity of hydroperiods in a landscape can we protect amphibian biodiversity (Semlitsch 2000).

Wetland hydroperiod and size were positively correlated in this study; however, the relationship between species richness and wetland size was

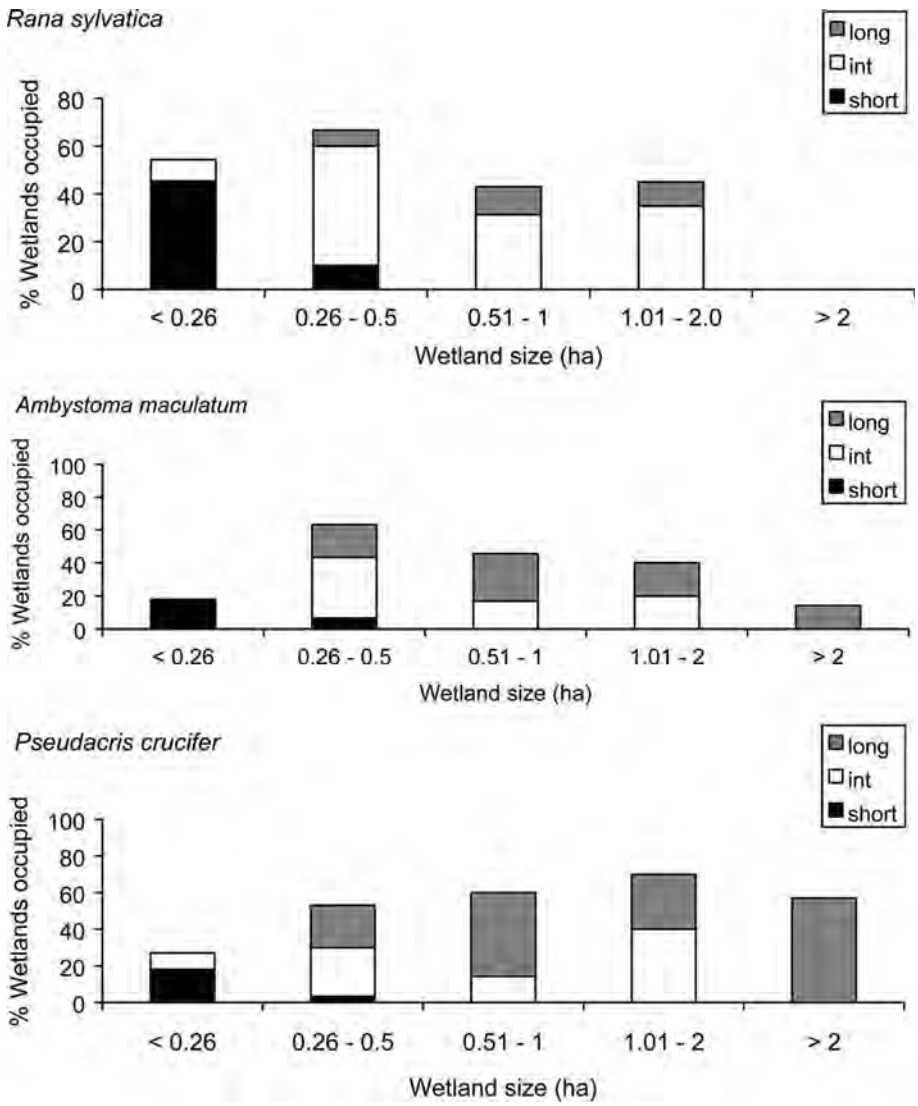
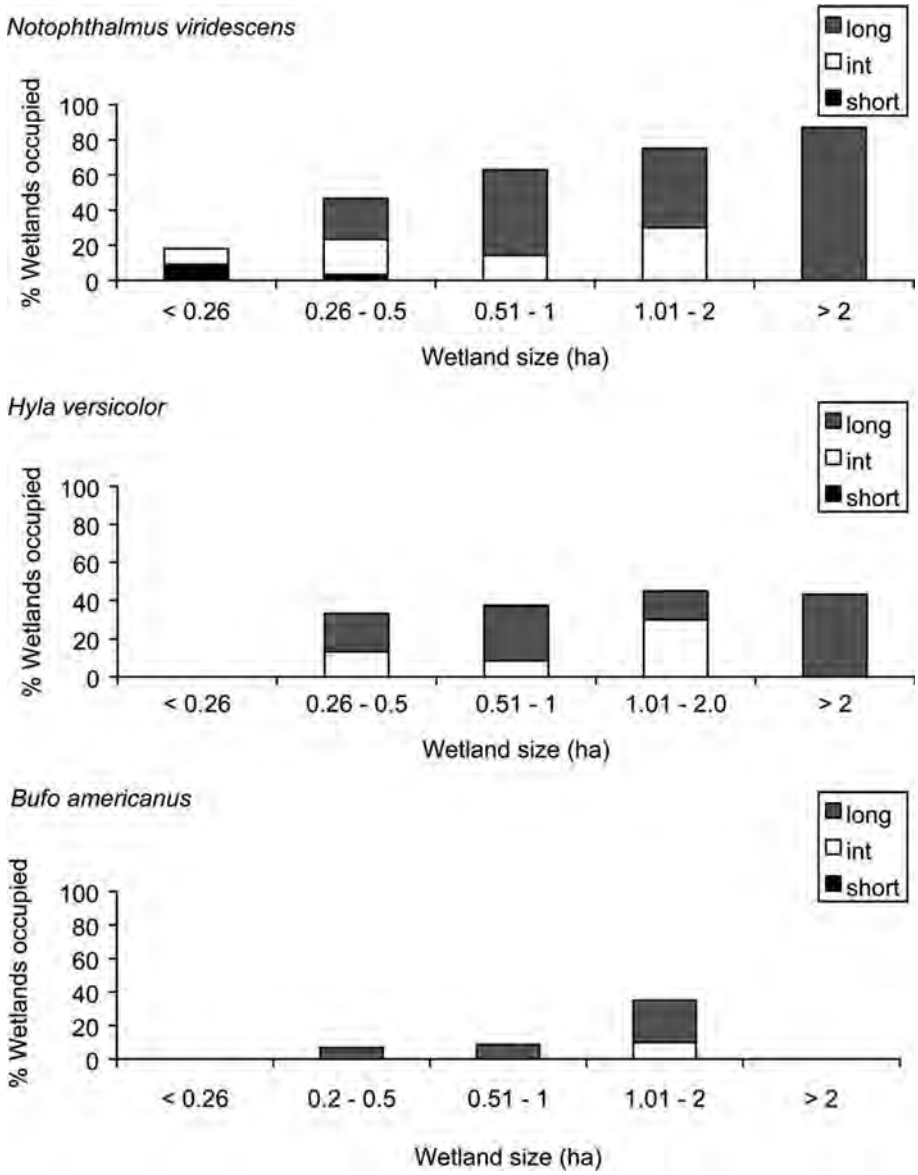


Figure 4. Patterns of occupancy of amphibian species in wetlands based on wetland size and hydroperiod. Hydroperiod was classified as: short (inundated <4 months), intermediate (inundated >4 months, nonpermanent), and long (permanent).

stronger in non-permanent wetlands. Because I was not able to determine the hydroperiod of each wetland on a frequent basis, I placed wetlands into hydroperiod categories. Thus, relationships between wetland size and amphibians occurrence and species richness within hydroperiod categories may be due to the fact that larger wetlands within, for example, the short hydroperiod category may have had longer hydroperiods than the smaller wetlands within that category (e.g., three months versus four months). Thus, a more detailed examination of hydroperiod/wetland size/species richness patterns, particularly among seasonally inundated wetlands, would be instructive.

Although only a few published studies have examined the relationship between hydroperiod, wetland size, and amphibian species richness, the findings of these studies suggest strongly that hydroperiod is a more valuable criterion for assessing wetland value for amphibians than wetland size. Snodgrass et al. (2000) found that wetland size and hydroperiod were positively but weakly (r^2 = 0.05) related among 86 wetlands at the Savannah River Site in South Carolina. They sampled a



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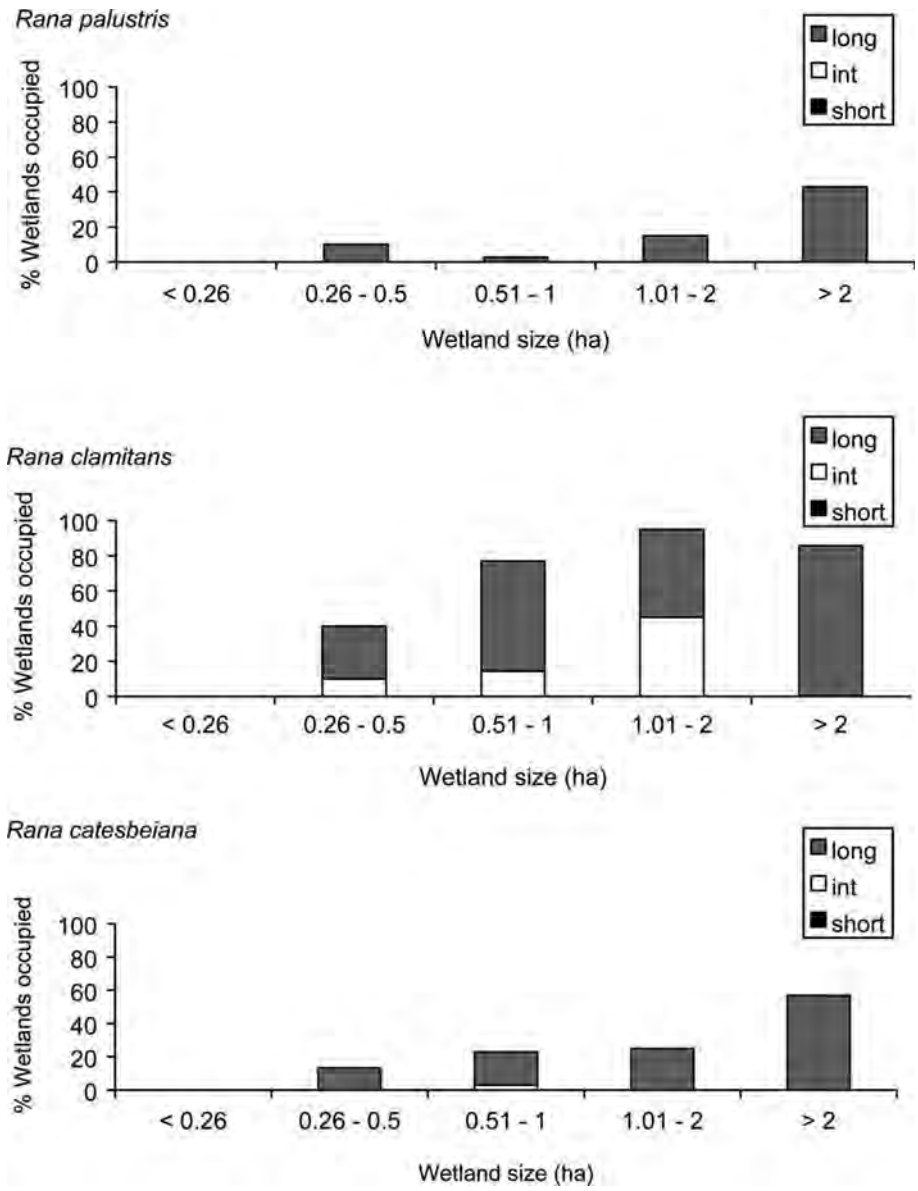
subset of those wetlands for amphibians and found that species richness was related to hydroperiod but not wetland size. In southern Ontario, Canada, Hecnar and M'Closkey (1996) found that amphibian species richness and pond size was not related in 97 ponds. Similarly, Richter and Azous (1995) did not find a significant relationship between wetland size and amphibian species richness among 19 wetlands in Washington State. Calhoun et al. (2003) found that neither wetland size nor depth was a reliable predictor of hydroperiod among over 300 isolated wetlands in different areas of Maine. As part of a test of a proposal for placing significance values on wetlands based on egg mass numbers for vernal-pool dependent amphibians, Calhoun et al. (2003) concluded that wetland size was a poor metric for assessing wetland value. Based on egg mass counts of *R. sylvatica* and *A. maculatum* at 124 ponds in Rhode Island, Egan and Paton (2004) found that selection of breeding sites was random relative to pond size; mean egg mass counts for ponds < 0.2 ha did not



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differ from those for ponds >0.2 ha. Combined, the results of these studies and the current study strongly suggest that wetland size is a poor criterion upon which to make decisions about wetland protection for amphibians.

An additional concern about the use of size as a basis for wetlands regulation is the fact that small, isolated wetlands can be quite numerous in certain areas of the United States (Tiner et al. 2002), and the loss of these wetlands could result in disruption of migration and gene flow among populations. For example, Semlitsch and Bodie (1998) examined size distribution patterns of Carolina bays at the Savannah River site in South Carolina and found that almost 50% of wetlands were less than 1.2 ha in size. Their analyses demonstrated that loss of wetlands below that size threshold would result in nearest-wetland distances that are beyond the dispersal limits of many amphibians. Similar analyses conducted on wetlands in Maine (Gibbs 1993) and New York (Gibbs 2000) also suggest that losses of small wetlands are likely to lead to

increased isolation of remaining wetlands, thereby increasing extinction probabilities of remaining amphibian populations.

In this study, four species were found in wetlands below 0.25 ha, and all nine species encountered used wetlands that were between 0.25 and 0.5 ha. Wetlands below 0.5 ha are of particular importance to *R. sylvatica* and *A. maculatum*. These sizes are smaller in area than is generally discussed at the federal level for wetlands protection (Kaiser 1998). Further, the US Supreme Court ruling in SWANCC (Solid Waste Agency of Northern Cook County vs. US Army Corp of Engineers, 531 US 159; 2001) which defined isolated wetlands as non-jurisdictional, and therefore not under federal permit review unless they were connected to a US navigable waterway, provides an additional challenge to protection of small, isolated wetlands. Although this court case has prompted some states to write new laws to regain legal authority to protect isolated wetlands, currently half the states in the United States do not have programs that address the reduction in federal jurisdiction (Christie and Hausmann 2003). Should this ruling stand, protection of 'isolated' wetlands will rest at the state level. States should respond not only by passing legislation to protect isolated wetlands, but also by protecting small wetlands.

The success or validity of policies and regulations centered around wetland size is dependent on the degree to which hydroperiod and wetland size are correlated, which is likely to vary among regions (e.g., this study versus Snodgrass et al. 2000). Because amphibian species composition changes with wetland hydroperiod, a strong correlation between hydroperiod and wetlands size argues for protecting wetlands of varying sizes. Lack of correlation between hydroperiod and wetland size argues against using size as a criterion at all. Overall, research to date suggests that wetland size should not be used as the sole metric for wetland protection, and further that small, isolated wetlands should be protected to ensure maintenance of amphibian biodiversity.

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