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**EVALUATING AMPHIBIAN OCCURRENCE MODELS AND THE
IMPORTANCE OF SMALL, ISOLATED WETLANDS IN THE DELAWARE
WATER GAP NATIONAL RECREATIONAL AREA**

A Dissertation in

Ecology

by

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ABSTRACT

Isolated wetlands lack permanent stream connections to adjacent bodies of water, and are ecologically important because they can be the most abundant type of wetland in a region, and can harbor unique biological communities. Despite this, isolated wetlands are rarely protected by federal and state legislation, and federal agencies do not assess their abundance when reporting national trends in wetland losses. In this dissertation, I present the results from a field study that illustrates how the presence of small and isolated wetlands is important in maintaining populations of pond-breeding amphibians across the Delaware Water Gap National Recreational Area located in New Jersey and Pennsylvania. I found that stream connections at wetlands strongly influenced the occurrence patterns of five out of nine amphibian species studied, and species that bred earlier in the year were the most likely to occur at small and isolated wetlands. I used occurrence patterns at surveyed wetlands to predict the presence of amphibian species across the entire study area, and estimated that two-thirds of all species would lose at least half of their breeding sites if either isolated wetlands or small wetlands (< 0.30 ha in size) were removed from this landscape. I also characterized the abundance and sizes of isolated and non-isolated wetlands that could serve as amphibian breeding sites, and modeled the probability these wetlands were detected on wetland maps as a function of their size. I found the majority of wetlands were small (< 0.5 ha) and isolated, and this trend was similar to several landscapes in the northeastern United States. Thus, if these landscapes were to follow national trends in wetlands loss, approximately 21 wetlands smaller than 0.5 ha could be degraded or destroyed for every wetland larger than 0.5 ha. Furthermore, I estimate this disparity could be twice as large because the rate small wetlands in this study area were included on wetland maps was considerably lower than inclusion rates for larger wetlands.

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INTRODUCTION

Geographically isolated wetlands (i.e., isolated wetlands) are completely surrounded by upland at the local scale and lack apparent surface water connections to perennial rivers and streams, estuaries, or the ocean (Tiner 2003a, 2003b). Isolated wetlands are the most abundant type of wetland in many landscapes across the United States (Tiner 2003b), and are ecologically important because they can contain highly diverse plant and animal communities that include species rarely found in non-isolated wetland types (reviewed by Liebowitz 2003, Comer et al. 2005). No vertebrate taxa are as intimately associated with isolated wetlands as amphibians, and many amphibian species adapted to breed in seasonally-flooded wetlands (notably Family Ambystomatidae) are found most often in isolated wetland types (Colburn 2004). Despite the importance of isolated wetlands, few are afforded federal protection because isolated wetlands, by definition, lack permanent stream connections to adjacent waterbodies. Furthermore, tracking the status and trends of isolated wetland abundance on a national level is difficult because many are too small to detect on aerial photography, and national trends in wetlands loss are typically expressed in the context of a wetland classification system that is based primarily on vegetation types. As a result, there has been an increased effort in academia, state and local governments, and non-governmental organizations to study and conserve isolated wetlands (Christie and Hausmann 2003, Calhoun and Reilly 2008, Mahaney and Klemens 2008).

DEFINITION AND ECOLOGICAL IMPORTANCE OF ISOLATED WETLANDS

Isolated wetlands typically occur in concave topographic depressions, and either completely lack stream connections to adjacent waterbodies, or have connections that dry during some part of the year due to seasonal fluctuations in surface water levels. It can be difficult to determine their abundance in a landscape from the scientific literature because scientifically accepted classification systems often place isolated wetlands into more than one fundamental category of wetland. Within the Hydrogeomorphic Wetland Classification System (Brinson 1993) that classifies wetlands by topography, landscape position, and primary water source, most isolated wetlands would be considered

Depression-type wetlands, although some Flat and Slope wetlands could be considered isolated also (Comer et al. 2005). Isolated wetlands could be classified as any of the nine classes of Palustrine wetland within the Cowardin Wetlands Classification System (Cowardin et al. 1979) because this system categorizes lentic wetlands by vegetation type. Using their standardized classification of 276 regional types of “natural/near natural” wetlands in the United States, NatureServe classified 29% of wetland types as being isolated wetlands (Comer et al. 2005).

The U.S. Fish and Wildlife Service (USFWS) has assessed national trends in wetland area for each decade since the 1970's (Dahl 1990, 2000, 2006). However, these data provide little insight into the abundance and loss of isolated wetlands because trends are expressed within the context of the Cowardin classification system. Furthermore, since the USFWS national wetlands database (The National Wetlands Inventory; NWI, <http://www.nwi.fws.gov>) also uses the Cowardin system to classify wetlands, investigators need to augment the NWI with other data sources in order to estimate the extent of isolated wetlands in study areas. This approach was taken by Tiner (2003b) who constructed a Geographic Information System (GIS) of 72 study areas across the United States (including 44 states and 20 ecoregions) using NWI data and U.S. Geological Survey digital raster graphics and digital line graph data. Tiner found that isolated wetlands often accounted for a large fraction of wetlands in a study area, even if they didn't account for the majority of total wetland area. Specifically, the number of isolated wetlands was greater than the number of non-isolated wetlands among 60% of the study areas, whereas the amount of isolated wetland area was greater than the amount of non-isolated wetland area among only 11% of the study areas. While this represented a wide-ranging survey of isolated wetlands across the U.S., it is unlikely this study accounted for a large proportion of small, isolated wetlands because the minimal mapping unit of the NWI database is 0.4 ha for open water and emergent wetlands in deciduous forest habitats (Tiner 1990).

Research conducted on seasonal ponds could be used to understand the distribution and ecological processes of small isolated wetlands (< 0.5 ha in area) since seasonal pools are

isolated wetlands that lack standing water during some portion of the year. Seasonal ponds are also referred to as ephemeral, temporary, vernal (Spring-filling), or autumnal (Fall-filling) ponds, with the terms “pool” and “pond” used interchangeably because there is no accepted size criteria to differentiate the two (Brooks et al. 1998). The primary geologic processes that resulted in the high abundance of small isolated wetlands currently witnessed across the northeastern U.S. was the expansion and retreat of the Late-Wisconsin glaciation (35,000 - 10,000 year BP), followed by 2,000 years of periglacial climate (reviewed by Rheinhardt and Hollands 2008). In central Maine, Calhoun et al. (2003) reported seasonal pond densities of 1.4 ponds/km², whereas the southern portion of the state had densities of 13.5 ponds/km². In study areas in Massachusetts, seasonal pool densities have ranged from 1.1 ponds/km² (Brooks et al. 1998) and 1.9 ponds/km² (Stone 1992), to 5.8 ponds/km² (Portnoy 1987). Seasonal ponds are typically smaller than 0.2 ha in size, with more than 80% of seasonal ponds being smaller than 0.1 ha in size for some study areas (Calhoun et al. 2003 and Brooks et al. 1998). Due to their small size, 1:4,800 aerial photography is examined to identify seasonal ponds across the landscape (Calhoun et al. 2003, Stone 1990), although the examination of 1:12,000 has been successfully used to identify these habitats (Brooks et al. 1998).

Large isolated wetlands can be important staging and feeding areas for migratory waterfowl (reviewed by Leibowitz 2003), but amphibians are often the most conspicuous, and most studied, vertebrate taxa found in isolated wetlands and seasonal ponds (Mitchell et al. 2008). In the northeastern and mid-Atlantic U.S., species of amphibians that breed most often in seasonal, isolated wetlands include the frog species *Rana sylvatica* (wood frog) and *Pseudacris crucifer* (spring peeper), and “mole salamander” species in the Family Ambystomatidae (Colburn 2004). These species have evolved life history strategies for breeding in seasonal waters that are akin to the Group 3 life history described by Williams (1983), Group 4 of Wiggins et al. (1980), and the “migratory breeder” life history more recently described by Colburn (2004). These strategies are typified by amphibian species whose adults inhabit upland habitats surrounding seasonal ponds during the majority of the year, then embark upon seasonal migrations during the

flooded phase of ponds in late winter or early spring to breed and deposit their eggs in the water. Aquatic larvae hatch from these eggs, and have developmental rates that are rapid enough to complete metamorphosis into terrestrial forms prior to the pond drying in the summer. The migration distances to breeding ponds for several amphibians typically exceed 200 m (Semlitsch and Bodie 2003), and amphibian species can have a strong tendency to return to their natal pond to breed as adults, and even stronger tendencies to breed in the same pond throughout their lifetime (Oldham 1966, Breden 1987, Berven and Grudzien 1990).

LEGISLATIVE PROTECTION AND CONSERVATION OF ISOLATED WETLANDS

Federal protection of isolated wetlands through the Clean Water Act (CWA) was fundamentally diminished with the U.S. Supreme Court decision in *Solid Waste Authority of Northern Cook County v. United States Army Corp of Engineers* (531 U.S. 159, 2001) (i.e., *SWANCC*). In *SWANCC*, proponents of a narrower definition of CWA-protected waters successfully argued that providing habitat for migratory birds was not sufficient evidence to warrant federal protection of a wetland because it was too tenuous of a link to the Commerce Clause of the U.S. Constitution. Since the CWA derives its authority through the Commerce Clause, the majority opinion in *SWANCC* ruled the only isolated wetlands the federal government had jurisdiction over were ones that were 1) adjacent to navigable waters, 2) adjacent to tributaries of navigable waters, or 3) had a significant nexus with navigable waters. The court, however, did not offer definitions of *adjacent*, *tributary*, or *significant nexus* in this decision, and these definitions were argued in *Rapanos vs. U.S. Army Corps of Engineers* (126 S. Ct. 2208, 2006).

The *Rapanos* decision failed to produce a majority opinion, resulting in a final vote of 4 to 1 to 4. Justice Scalia wrote the plurality opinion for the Court, and proposed that isolated wetlands could only be protected by the CWA if they displayed “relatively permanent” flow into a tributary of a navigable body of water (i.e., a connection lasting at least three months). Therefore, the plurality opinion supported elimination of the *significant nexus* criteria offered in *SWANCC*. In a separate, non-dissenting opinion, Justice Kennedy proposed to retain the spirit of the *significant nexus* criteria, and that

CWA protection should be given to any wetland that impacts the chemical, physical, and biological integrity of a tributary to a navigable body of water. Since a majority decision was not reached in *Rapanos*, an isolated wetland could be protected under the CWA if it met the criteria set forth by either Justice Scalia or Justice Kennedy. In this decision, the Court essentially placed the onus on federal agencies (i.e., the U.S. Environmental Protection Agency and U.S. Army Corps of Engineers) to establish guidelines on which seasonal hydrologic connections constitute a significant nexus to a navigable body of water.

Barring congressional amendments to the CWA that explicitly establishes the protection of all wetlands, the legislative protection of isolated wetlands will largely fall in the hands of state, local, and tribal governments. Currently, 15 states have wetland permitting programs akin to CWA, and the majority of these states are located in the northeast U.S. (e.g., Connecticut, Maine, Massachusetts, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island, and Vermont) (Christie and Hausmann 2003, Mahaney and Klemens 2008). Within this region, all nine states give jurisdictional status to isolated wetlands without requiring adjacency to navigable waters (or their tributaries), and all but one (New York) have no size requirements to grant jurisdictional status to wetlands. Furthermore, Connecticut, Massachusetts, and New Jersey have specific language in their state regulations to include the protection of isolated wetlands, and have partnered with academic institutions and citizen-science programs to locate, inventory, and map isolated wetlands (Lathrop et al. 2005, Burne and Griffin 2005b). Although these programs can face significant challenges in assembling and sharing data, prioritizing the protection of individual isolated wetlands by their conservation value can be equally challenging (Mahaney and Klemens 2008). Most isolated wetland inventory programs prioritize pools by the occurrence and abundance of amphibian populations that typically breed in seasonal ponds. However, in order to prioritize wetlands on their potential to ensure the persistence of amphibian populations, programs will have to consider both the hydrologic characteristics of the wetlands themselves, and the condition of adjacent upland habitats (Mahaney and Klemens 2008).

THIS STUDY'S CONTRIBUTION TO THE CONSERVATION OF ISOLATED WETLANDS

In the spring of 2005, I initiated a study to evaluate the importance of small and isolated wetlands in maintaining pond-breeding amphibian populations throughout the New Jersey portion of Delaware Water Gap National Recreation Area (NJ-DEWA). To accomplish this I: 1) produced a map of all wetlands that could serve as breeding habitats for amphibians, 2) developed statistical models to predict the occurrence of amphibian species at all NJ-DEWA wetlands, and 3) quantified potential impacts on breeding wetland abundance and spatial isolation as a result of the loss of small wetlands and isolated wetlands in the landscape.

In Chapter 1, I present occupancy models (MacKenzie et al. 2002) for nine species of pond-breeding amphibians to predict their occurrence at wetlands as a function of wetland size, upland forested habitat, hydrologic connectivity to adjacent wetlands, and the spatial isolation to adjacent wetlands. Island biogeography would predict that larger wetlands should contain more amphibian species than smaller ones, yet several studies on amphibian communities have found no correlation between size and species richness (Hecnar and M'Closkey 1996, Lehtinen and Galatowitsch 2000, Snodgrass et al. 2000, Weyrauch and Grubb 2004). However, these studies often fail to characterize hydrologic connectivity, or they sample wetlands with similar hydrologic connections. To address this shortcoming, I framed wetland size within the context of a hydrologic connectivity when predicting species occurrences. In addition, separate model validation data were used to assess the accuracy of model predictions in wetlands outside of the study area. If hydrologic connectivity is an important and reliable predictor of species occurrence, then wetland inventory programs should explicitly assess hydrologic connectivity because it could be useful criteria to prioritize the importance of individual isolated wetlands.

The map of potential breeding wetlands that I constructed for NJ-DEWA allowed me to compare the distribution and abundance of isolated wetlands to the distribution of non-isolated wetlands. This is an important comparison because many comprehensive inventories of small (< 0.5 ha), isolated wetlands in the northeastern U.S. do not compare their results to the relative abundance of non-isolated wetlands. In Chapter 2, I used

occupancy models derived in Chapter 1 to predict species occurrences at all potential breeding wetlands in NJ-DEWA. I used these predicted occurrence patterns to estimate: 1) the number of breeding wetlands and 2) the total amount of breeding wetland area in NJ-DEWA for nine species of amphibians. To identify amphibian species that would be impacted the greatest by the loss of small wetlands and isolated wetlands, I tracked the loss of predicted breeding wetlands and their increased degree of spatial isolation under scenarios where: 1) wetlands of increasing size, and 2) isolated wetlands were removed from NJ-DEWA. I expect that species that conform to the “seasonal migrant” life history strategy (Colburn 2004) will be impacted the greatest by the loss of small and isolated wetlands because these habitats tend to dry in the summer months, and “seasonal migrant” species have larvae with developmental rates that are rapid enough to complete metamorphosis in these wetlands. Furthermore, these species will be less likely to use large, non-isolated wetlands because their larvae are more susceptible to predation by aquatic predators that inhabit permanent bodies of water (Woodward 1983, Wilbur 1987).

The hydroperiod of an isolated wetland can be an important factor in determining its ecological function, as well as its protective status under state laws. Although wetland size (Snodgrass et al. 2000, Bilton et al. 2001, Brooks and Hayashi 2002, Skidds and Golet 2005) and water chemistry parameters (Skidds and Golet 2005) have been used to predict wetland hydroperiod, these studies fail to account for differences between isolated wetlands that lack stream connections, and those with seasonal connections. Therefore, in Chapter 3, I compare how the relationships between wetland size, drying regime, and water chemistry parameters differ according to the wetland’s degree of hydrologic connectivity. I expect that wetlands with more permanent stream connections will have surface waters that persist longer and have higher pH and conductivity than isolated wetlands because the relative contribution of groundwater to wetland water budgets generally increase with hydrologic connectivity (Biggs et al. 1994, Cole et al. 1997, Gay 1998, Cole and Brooks 2000).

Parties involved in the inventory and monitoring of isolated wetlands may rely on publicly available wetland maps to locate these habitats, and knowing omission and

commission error rates of these maps could help them develop program goals. Although it is assumed that small wetlands are difficult to detect on wetland maps derived from aerial photography, the relationship between wetland size and omission error rates has not been modeled in studies where isolated wetland abundance is high. In Chapter 4, I model the probability small breeding wetlands would be omitted from publicly available GIS wetland databases (based on 1:58,000 and 1:12,000 aerial photography), and examine ways to identify breeding wetlands among all wetland polygons contained in these databases. In Chapter 4, I also evaluate the potential to increase the number of breeding wetlands detected by these datalayers using an airborne light detecting and ranging (LiDAR) sensor. To determine whether LiDAR mapping is less biased towards the omission of small wetlands than aerial photography, I compare the accuracy of LiDAR predictions between wetlands detected on GIS wetland databases, to those omitted from databases.

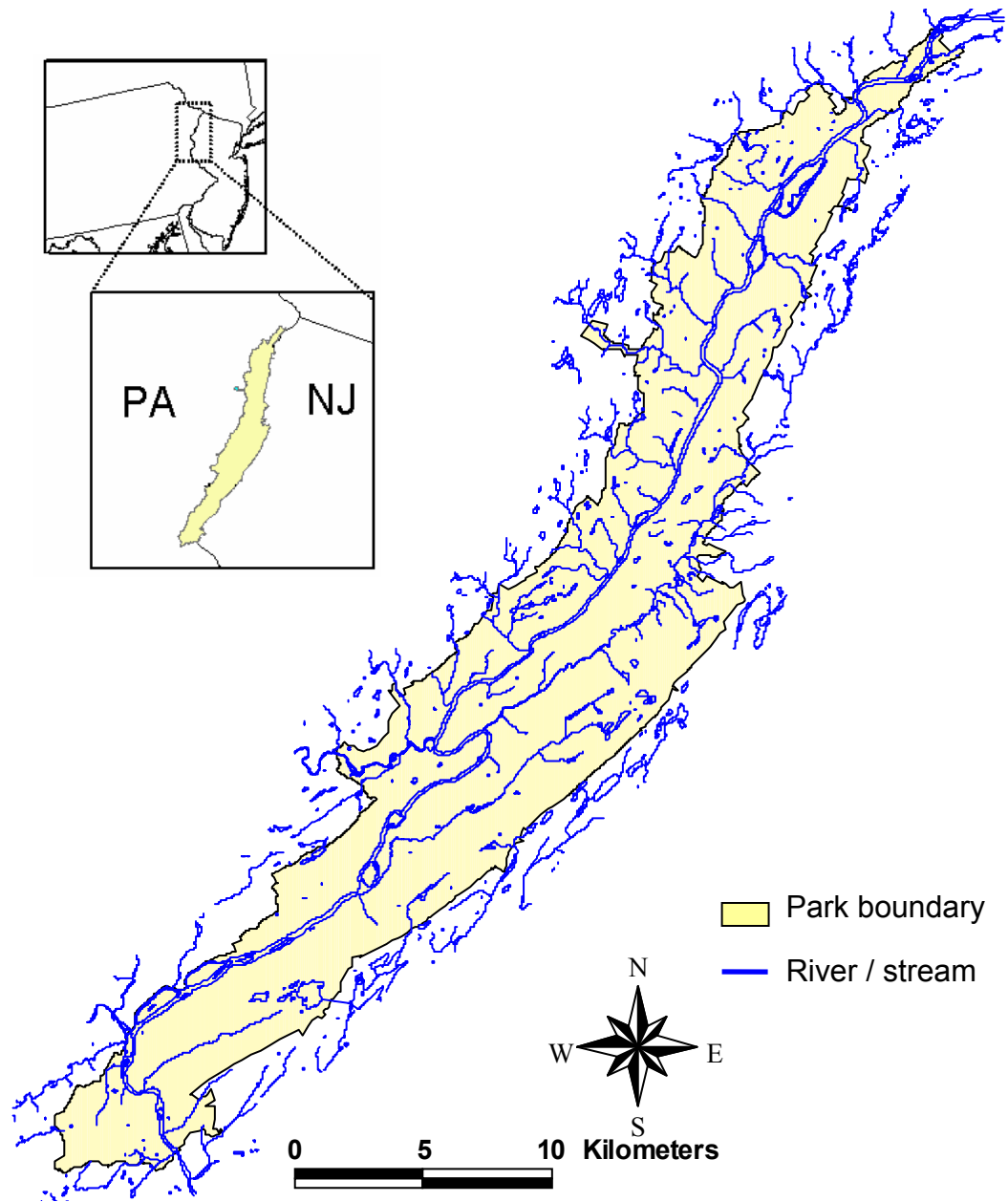


Figure 0.1. Map of Delaware Water Gap National Recreation Area. Inset shows the location of the park within the states of Pennsylvania (PA) and New Jersey (NJ).

CHAPTER 1:

Predicting amphibian occurrence across gradients of wetland size,
hydrologic connectivity, and geographic isolation

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ABSTRACT

Considerable research has been directed at understanding the functional relationships between the presence of pond-breeding amphibians and wetland size, upland terrestrial habitat, and the spatial isolation of wetlands. However, most efforts have not considered the potential role that hydrologic connections between individual wetlands and permanent and non-permanent streams (hydrologic connectivity) might play in determining habitat suitability for pond-breeding amphibians. Our research in the Delaware Water Gap National Recreation Area, USA (DEWA) suggests that hydrologic connectivity (CONNECT) is important in explaining the occurrence patterns for five out of nine species of pond-breeding amphibians that occur in DEWA. For two of the five species, *Pseudacris crucifer* and *Rana palustris*, hydrologic connectivity was the most significant predictor of occurrence and strongly influenced the functional relationship between the probability of occurrence and wetland size in a non-additive manner. Hydrologic connectivity was related to wetland hydroperiod and the occurrence of predatory fish, two variables known to be major factors that influence the reproduction and persistence of amphibian populations, but which are often difficult to quantify without considerable field effort. In contrast, assessment of hydrologic connectivity can potentially be assessed using digital hydrologic and topographic data in a Geographic Information System environment, or on a single field visit through the use of widely accepted wetlands classification systems. Models of species occurrence were adjusted by our ability to detect each species during surveys, and they generated relatively accurate predictions of species occurrence (% correct classification ranged from 62.5% to 90.6%) when validated using observations at 32 model validation sites.

INTRODUCTION

As a group, amphibians are experiencing alarming declines at global, regional, and local scales (Stuart et al. 2004), and researchers have identified habitat destruction and alteration (Wake and Morowitz 1991, Blaustein et al. 1994, Delis et al. 1996, Hecnar and M'Closkey 1996, Dodd 1997, Alford and Richards 1999), predator introductions (Bradford et al. 1993, Knapp and Matthews 2000, Vrendenburg 2004), and disease outbreaks (Daszak et al. 2003, Lips et al. 2006, Pounds et al. 2006) as proximal causes of observed declines. In order to protect amphibians, it is critical that resource managers are able to identify critical breeding habitats in order to assess species status, quantify biodiversity, and anticipate potential impacts on amphibian species and assemblages.

Both island biogeography theory (MacArthur and Wilson 1967) and metapopulation theory (Levins 1970, Hanski 1999) predict a positive relationship between species presence and both habitat size and persistence, yet empirical evidence suggests these predictions do not always hold for pond-breeding amphibian assemblages. For example, wetland size is not always correlated with amphibian species richness (Hecnar and M'Closkey 1996, Lehtinen and Galatowitsch 2000, Snodgrass et al. 2000, Weyrauch and Grubb 2004), and amphibian species richness has been found to be highest in wetlands with intermediate hydroperiods for some study systems (Kolozsvarly and Swihart 1999).

Several mechanisms have been proposed that explain these deviations from theoretical predictions, and that are supported by empirical observations. Perhaps most important, is the propensity for larger wetlands with longer hydroperiods to contain more abundant and diverse populations of aquatic predators (Woodward 1983, Schneider and Frost 1996, Skelly 1996), particularly fish, that can prevent some amphibian species from reproducing (Resetarits and Wilbur 1991, Kats and Sih 1992, Hopey and Petranka 1994) or persist in wetlands (Knapp and Matthews 2000, Larson and Hoffman 2002). Second, there is strong evidence that occurrence patterns in many pond-breeding amphibian species are related to characteristics of clusters of ponds or wetlands within an area rather than to individual wetlands (Semlitsch and Skelly 2008). Thus, the probability of occurrence for a species or overall species richness may be high even in a small wetland

if there are many other ponds or wetlands nearby. This landscape perspective is reinforced by the preponderance of studies that have reported strong correlations between species occurrence and richness with measures of spatial isolation such as; mean distance to other wetlands (Sjögren 1995, Lehtinen et al. 1999, Lehtinen and Galatowitsch 2000), the number of wetlands within a given area around a wetland (Vos and Stumpel 1996), and the total amount of wetland acreage within a given distance (Findlay and Houlihan 1997, Vos and Chardon 1998, Knutson et al. 1999) Finally, the quality of a breeding site is at least partly determined by the quality of terrestrial habitat nearby. Specifically, maintaining upland forested habitats appears to be vital to the conservation and management of pond-breeding amphibian species (Semlitsch 2000, Skelly 2001, Semlitsch 2002, Gibbons 2003) because they are positively associated with species occurrence (Guerry and Hunter 2002, Porej et al. 2004, Rubbo and Kiesecker 2005) and species richness (Findlay and Houlihan 1997, Hecnar and M'Closky 1998, Knutson et al. 1999, Rubbo and Kiesecker 2005) at multiple spatial scales. Taken together, these observations suggest that the suitability of an individual pond or wetland as a breeding site is determined to some extent by how isolated individual wetlands are from other wetlands, and other components (e.g., upland forests) of the landscape.

Hydrologically isolated wetlands are a special case of wetland habitat that lack stream connections to other surface-water bodies (Winter and LaBaugh 2003). Protection of isolated wetlands is important because over one third of all wetland habitat types are considered isolated wetlands, as well as 13% of all terrestrial habitat types (Comer et al. 2005). Isolated wetlands also harbor an estimated 86 federally protected species that can be found in 43% of all isolated wetland types (Comer et al. 2005). Furthermore, isolated wetlands function as waterfowl staging and stopover points, can maintain metapopulation dynamics for some species, and can harbor fauna that are highly diverse and endemic (reviewed by Leibowitz 2003). Despite their ecological importance, isolated wetlands do not fall under the federal protection of the U.S. Clean Water Act unless they are 1) adjacent to navigable waters, 2) adjacent to tributaries of navigable waters, or 3) have hydrological, biological, or ecological connections that display a significant nexus with navigable waters or their tributaries.

Isolated wetlands may be especially important to pond-breeding amphibians because the larval stages of many species can not coexist with predatory fish that are more prevalent in less isolated, perennial habitats. However, most previous efforts to explain the richness, abundance, and occurrence of pond-breeding amphibians have not considered the role of hydrologic connectivity. As a result, investigators fail to describe the influence of a legislatively relevant wetland characteristic on amphibian species distributions and the ways this characteristic interacts with other environmental conditions that influence amphibian species composition in wetlands. Although isolated wetlands can exceed half of the total wetland acreage and abundance in some landscapes in the U.S. (Tiner 2003b), management areas will typically contain both isolated and other wetlands. Thus, resource managers may have an incomplete picture of the status and potential threats to amphibian populations if they fail to describe the inherent relationship between amphibian species presence and hydrologic connectivity.

In the spring of 2005, we initiated a study to develop spatially-explicit models to predict the occurrences of nine species of pond-breeding amphibians in wetlands that vary widely in size, spatial isolation, and hydrologic connectivity within Delaware Water Gap National Recreational Area, USA (i.e., DEWA). Evidence of breeding activity was used to create models for the following pond-breeding amphibian species: spotted salamander (*Ambystoma maculatum*), red-spotted newt (*Notophthalmus viridescens*), American/Fowler's toad (*Bufo* species), Northern gray treefrog (*Hyla versicolor*), spring peeper (*Pseudacris crucifer*), American bullfrog (*Rana catesbeiana*), green frog (*Rana clamitans*), pickerel frog (*Rana palustris*), and wood frog (*Rana sylvatica*). Important to these models was the use of a legislatively relevant assessment of hydrological connectivity that can be easily assessed in the field and, if necessary, from available Geographic Information System (GIS) datalayers and wetland classification systems commonly used by the scientific community. Furthermore, this assessment conferred information on important abiotic (hydroperiod) and biotic (predator presence) conditions that shape amphibian assemblages. Finally, separate training and validation data sets were used to quantify the accuracy and exportability of models that accounted for the probability that species were present, but not detected during surveys.

METHODS

Study Area and Prior Mapping of Amphibian Habitats

DEWA consists of nearly 28,000 ha of mostly forested habitat along the Delaware River in northeastern Pennsylvania (PA) and northwestern New Jersey (NJ). The park contains hundreds of bodies of water that include a variety of wetland types: natural depressions, beaver ponds, and artificially impounded open water ponds and vegetated wetlands. During the years 2001 through 2003, we conducted surveys of amphibian breeding habitats in the park and identified a total of 352 lentic (non-flowing) wetlands that typically possessed standing water through the month of April (when ambystomatid salamanders lay their eggs) (Snyder et al. 2004). We also surveyed approximately 200 randomly selected wetlands for pond-breeding, ambystomatid salamanders (Family: Ambystomatidae) and mapped wetland perimeters with handheld, global positioning systems (Trimble™ GeoXT unit) to obtain accurate estimates of their size during high-water conditions (typically mid-April). In addition to wetlands mapped in the field, we obtained areas for an additional 66 wetlands from the National Wetlands Inventory database (NWI, <http://www.nwi.fws.gov>) for large (> 1 ha) wetlands with relatively stable hydroperiods. Preliminary results from these surveys of 266 wetlands indicated that small wetlands constituted a significant portion of wetland abundance throughout the park. For example, wetlands < 1 ha constituted nearly 25% of all wetland area, and nearly 85% of the total number of wetlands.

We selected wetlands for amphibian surveys from a GIS datalayer of potential amphibian breeding wetlands in DEWA (Snyder et al. 2004) that were characterized by their size and degree of spatial isolation. We categorized the 181 potential amphibian breeding sites identified in NJ portion of DEWA according to three wetland sizes and three spatial isolation classes. The three wetland size classes included wetlands; 1) < 0.1 ha, 2) 0.15 – 0.66 ha, and 3) \geq 1.0 ha. We excluded wetlands that fell between these size classes to limit the possibility that extreme rainfall patterns would reassign a surveyed wetland into to different size classes. Furthermore, the distribution of all known wetlands in NJ-DEWA fell evenly across these categories (~ 1/3 in each size class). Spatial isolation was quantified as the number of wetlands within 1 km of each wetland's perimeter. Wetlands

were classified as having a high, medium, or low degree of spatial isolation if they contained 0-3 wetlands, 4-7 wetlands, or ≥ 8 wetlands within 1 km of their perimeters, respectively. Each isolation class represented approximately 1/3 of all wetlands in DEWA, and permitted us to sample at least three large wetlands (> 1 ha) in each of the three spatial isolation classes.

We used a stratified random design to select a total of 44 potential amphibian breeding wetlands in NJ-DEWA to survey for amphibians in 2005. We selected at least three wetlands within each *Size X Spatial isolation* class combination to ensure that survey sites represented all size and spatial isolation class combinations (Table 1.1). Wetlands surveyed in NJ-DEWA are considered “model training sites” because encounter histories of amphibian species at these sites were used to parameterize models that predict the presence of 9 amphibian species at 32 potential breeding wetlands in PA-DEWA, which were surveyed for amphibians in 2006. PA-DEWA sites were used as model validation sites.

We refined the GIS datalayer used in site selection with information from hydrological assessments and wetland mapping performed from 2005 through 2007. The updated potential amphibian breeding wetland datalayer included a total of 336 potential breeding wetlands in DEWA whose perimeters were either: 1) mapped in the field using GPS ($n = 217$), 2) incorporated from GIS datalayers of photo-interpreted wetlands ($n = 101$), or 3) represented by point locations of unmapped ponds ($n = 18$). This updated datalayer was used to estimate wetland areas and calculate spatial isolation metrics for all data analyses associated with amphibian occupancy models in this paper, and their associated predictions.

Amphibian Surveys

Each selected site in NJ-DEWA was surveyed for amphibians at least once per month from April through July of 2005 using a combination of visual encounter surveys (VES) (Crump et al. 1994), aquatic larvae dipnet surveys (dipnet surveys) (Shaffer et al. 1994), and anuran call surveys that were conducted during daylight hours (typically between

8:00 – 18:00 hrs). Time-constrained VES were performed at least once in April, and at least once in May, and each sampling ended when no new species were encountered during the last 10% of a sampling effort and either: 1) all areas of a wetland < 1.33 m in depth were searched or 2) the number of person minutes reached a maximum amount of effort (person minutes). The maximum amount of person minutes at a site was approximated by a function of the median perimeter of all wetlands within the site's size class (Equation 1).

Equation 1: $Maximum\ minutes\ surveyed_{size\ class} \approx 0.065 (median\ perimeter_{size\ class}) + 12\ minutes$

Aquatic dipnet surveys were conducted at least once per month in May through July, and consisted of one 1.5 m sweep with a D-frame net (50 x 50 cm head x 5mm size mesh) taken systematically every 10 m around the perimeter of the wetland until: 1) the entire wetland perimeter was traversed, 2) 100 sweeps were performed, or 3) 180 person minutes of sweeping was performed. A “low intensity” VES also was conducted concurrent with dipnetting to record species and life stages not captured with dipnet sweeps.

Anuran call surveys were conducted prior to each VES and dipnet survey. Upon arrival at a site, we stopped approximately 10 m from the edge of a wetland's flooded perimeter, listened for calling anurans for a period of 5 min, and recorded the identity of each species heard. Some anuran species are more likely to call during the daytime than others, and this could potentially affect their detectability. However, we used call surveys only to verify the breeding activity of *R. catesbeiana* because their larvae were the most difficult to capture in dipnet surveys.

At each survey we created an inventory of the life stages of amphibian species encountered (adults, egg masses, larvae, and calling adults), and recorded the relative abundance of each life stage on an ordinal scale (1-20 individuals, 21-100, and >100 individuals). In addition, we also created an inventory of aquatic predators of amphibians (fish, predatory beetles [Family Dytiscidae], predatory hemipterans [Family

Belostomatidae], dragonfly larvae [Order Odonata], and predatory caddis fly larvae [Family Phryganeidae]). Inventories were used to construct an encounter history of breeding stages (egg and larvae) of each amphibian species at each site across the entire survey period (from April through July). In addition, this protocol allowed us to create an encounter history for predatory fishes at each site.

In 2006, we performed amphibian surveys at 32 wetlands in PA-DEWA with the same protocols used to survey wetlands in NJ-DEWA. At each site, VES were performed twice in April and once in May, and dipnet surveys were performed once in May, and twice per month in June and July. Anuran call surveys preceded each VES and dipnet survey.

Hydrologic Regimes, Water Inputs and Wetland Assessments

For each selected wetland we assessed the hydroperiod, wetland size, and degree of hydrologic connectivity. We inferred hydroperiod by the pattern of water volume change through the breeding season. Specifically, on each sampling occasion, we assigned a drying score based on the observed area at the time relative to maximum area observed at the site (typically in mid-April). Drying scores were based on a fairly gross qualitative ranking as follows: 0% of maximum (dry), 1-10%, 11-50%, 51-90%, or > 90% of its maximum observed area (Julian et al. 2006). If surveyed wetlands displayed a fluctuating seasonal hydroperiod during previous studies (Snyder et al. 2004, Julian et al. 2006), we estimated their size by mapping their flooded perimeters in April of 2005 with a 12 channel, Trimble™ GPS mapping unit. The size of surveyed wetlands larger than 4 ha, as well as those with stable hydrologic regimes (ponds, artificial impoundments, etc.), were estimated using the GIS datalayer from Snyder et al. (2004).

We assessed the degree of hydrologic connectivity for each wetland surveyed. We classified wetlands on a ranked scale as being 1 = strictly isolated, 2 = seasonally connected, or 3 = permanently connected. Strictly isolated wetlands contained no channelized inflow or outflow of surface water. Seasonally connected wetlands possessed a seasonal hydrologic connection that consisted of inflows or outflows that

were observed to dry at least once during the year, whereas permanently connected wetlands had at least one channel that had never been observed as dry (even if they potentially could dry during prolonged periods of drought).

Amphibian Species Occupancy Models

Encounter histories for nine amphibian species at 44 sites in NJ-DEWA were used in occupancy models (McKenzie et al. 2002) to estimate the relationship between the probability of species occurrence and predictor variables associated with forest canopy cover, wetland size, hydrologic connectivity, spatial isolation of wetlands, and fish presence. Only two other species of pond-breeding amphibians were encountered at sites (*Ambystoma opacum* [marbled salamander] and *Ambystoma jeffersonianum* [Jefferson salamander]), but these species were encountered at too few sites to produce informative models. The presence of adults or small male choruses does not guarantee a site is being used for breeding; therefore, encounter histories for most species were constructed from encounters with their reproductive stages (either egg masses or larvae). The exception to this was the encounter histories of *R. catesbeiana*. Detection of this species was based on encounters with any life stage because *R. catesbeiana* larvae are exceptionally strong swimmers and are hard to detect, and the egg masses of this species are identical to those of *R. clamitans*.

Logistic regression is often used to predict amphibian species occurrence at wetlands, but makes the implicit assumption that all species present at a site are detected during surveys. If this assumption is false, logistic regression models can underestimate the probability a species will occur at a site or misidentify factors that influence species presence (Tyre et al. 2003, MacKenzie et al. 2006). In contrast, occupancy models do not assume species detection is perfect, and adjust the functional relationship between predictor variables and the probability of occurrence (ψ) to account for the probability that a species was actually present, but was not detected during surveys. Maximum-likelihood estimation is used to model the probability of detection (p) for a species by examining the encounter histories from sites where the species was detected at least once. Because maximum likelihood is used to estimate p and $\hat{\psi}$, both parameters can be

modeled as functions of site-specific and survey-specific covariates, statistical significance of covariates can be evaluated by examining the error terms of coefficients, and competing statistical models can be directly compared with model fit parameters such as Akaike Information Criteria (AIC) scores. Estimates of p and $\hat{\psi}$, and AIC scores were computed using the computer program PRESENCE v 2.0.

We quantified local conditions associated with wetland size, hydrologic connectivity, and the presence of fish. Values of wetland size (AREA) were obtained from the updated amphibian breeding wetland GIS datalayer and log transformed for analyses in occupancy models, whereas hydrologic connectivity (CONNECT) was entered in models as an ordinal variable (1 = isolated wetland, 2 = seasonal connection, 3 = permanent connection). The covariate for fish presence (FISH) was entered in models as a binary variable (0 = fish not detected, 1 = fish detected), where presence was determined by the detection of fish (regardless of species) during at least one survey of a breeding wetland.

We quantified the proportion of the area surrounding each wetland that contained at least 50% forest canopy cover within 25 m (P25), and within 250 m (P250) of their flooded perimeter. This was accomplished in a GIS environment with the updated amphibian breeding wetland datalayer and a photo-interpreted digital vegetation map of DEWA (Fike 1999; available at: <http://nrdata.nps.gov/dewa/dewadata/>) that delineated and attributed polygons according to their canopy cover class. Polygons with values of > 50% canopy cover were overlaid with 25-m and 250-m buffer areas surrounding amphibian breeding wetlands. The proportion of the area within each buffer that contained > 50% canopy cover was quantified, and these proportions were entered into occupancy models as continuous variables following an arcsin square-root transformation. The cutoff of 50% canopy cover was chosen because Gibbs (1998) failed to detect *N. viridescens* in forest patches with < 50% canopy cover, and failed to detect *R. sylvatica* and *A. maculatum* in patches with < 30% canopy cover. We chose 250-m buffer areas around ponds because this value approximates the average maximum migration distance of *A. maculatum* (248 m) (Semlitsch 1998), and this distance from seasonal pools is designated as critical upland habitat for vernal pool breeding

amphibians (Calhoun et al. 2005). We chose to characterize 25-m buffers around ponds because it was an order of magnitude smaller than our larger buffer size, and approximates the working definition of a vernal pool's seasonal riparian envelope of 30m (Brown and Jung 2005, Calhoun et al. 2005).

We quantified landscape-level metrics of spatial isolation associated with breeding wetland acreage, abundance, and proximity. We used the updated amphibian breeding wetland datalayer to quantify the number of potential breeding wetlands within 1 km of the flooded perimeter of each focal pond or wetland (PONDS1KM). Similarly, we quantified the sum total area of potential breeding wetlands located within 1 km of each wetland's flooded perimeter, then log-transformed these areas for analysis in occupancy models (AREA1KM). And lastly, we calculated the nearest edge-to-edge distance to the nearest potential breeding wetland (MINDIST). The Delaware River was considered an absolute migration barrier for amphibians, thus, all spatial isolation metrics were calculated using a restricted pool of neighbors that were located in the same state (Pennsylvania or New Jersey). Furthermore, spatial isolation metrics included data on potential breeding wetlands within 1 km outside of the park's boundaries to reduce "edge effects" associated with incomplete spatial data.

We employed a two-step approach for developing final occupancy models that incorporated covariates to predict both p and $\hat{\psi}$ at each breeding wetland. For each species, competing models of p with identical parameterizations of $\hat{\psi}$ (i.e. ψ (AREA, CONNECT, FISH, PONDS1KM, P250)) were compared to each other to determine the best-fit parameterization of p . Next, competing models of ψ that used identical best-fit parameterizations of p were compared to determine overall final occupancy models for each species. For both steps, models were selected from a pool of candidate models in which all parameters were estimable, and AIC scores were used to determine the most parsimonious model with a substantial level of empirical support (Burnham and Anderson 2002).

Competing models of p included combinations of time-dependent and time-independent detection probabilities with the covariates FISH, AREA, and FISHXAREA. By modeling p for each wetland surveyed, we were able to estimate the probability each species, if present, would be detected at a site during at least one survey (p^*). For each site, p^* is based on the actual number of times the site was surveyed, thus the average of p^* across all sites (\bar{p}^*) should then give us an idea of how thoroughly our survey protocols sampled each species.

Competing models for ψ were parameterized with combinations of the covariates AREA, CONNECT, PONDS1KM, AREA1KM, MINDIST, P250, P25, and the interaction term AREAXCONNECT. One of the main objectives of developing final models was to predict the occupancy states of species in all NJ-DEWA wetlands. Therefore, it was vital for us to test models that only contained variables that could be quantified at all NJ-DEWA wetlands (including those where amphibians were not surveyed). As a result, the covariate FISH was not used in candidate final occupancy models because fish presence was not recorded at NJ-DEWA sites where amphibian surveys were not performed. We did, however, evaluate the impact of fish presence on $\hat{\psi}$ for each species in the absence of CONNECT as a covariate of $\hat{\psi}$. This was done by either: 1) substituting the covariate FISH for CONNECT in final models of species that contained the covariate CONNECT, or 2) adding the covariate FISH to final models of species that did not contain CONNECT as a covariate.

We used a similar approach to model ψ for fish at surveyed NJ-DEWA sites. In a two-step process similar to amphibian occupancy models, we first modeled p in combinations of time-dependant and time-independent models with combinations of the covariates AREA, CONNECT, and the interaction term AREAXCONNECT. Best-fit models for p were then used in subsequent models of ψ that were parameterized with combinations of the covariates AREA, CONNECT, and the interaction term AREAXCONNECT.

Evaluating Model Fit for Species Occupancy Models

To assess the accuracy of model predictions, we compared the predicted occupancy states (presence or absence) for the nine species of amphibians to their observed detections at sites surveyed in NJ-DEWA (model training data set) and sites surveyed in PA-DEWA (model validation data set). Final occupancy models were used to predict $\hat{\psi}$ for each species at each NJ-DEWA site sampled. If the predicted $\hat{\psi}$ for a species exceeded 0.5 at a model training site, the species was predicted to occur there. Four measures of accuracy were calculated at each site: percent correct classification, sensitivity, specificity, and concordance. The percent of correctly classified sites is the proportion of all sites where either: 1) species were detected and predicted to occur or 2) species were not detected and predicted to be absent. Sensitivity is the fraction of sites where the species is predicted to occur, out of all sites where the species was detected. Specificity is the fraction of sites where the species is predicted to be absent, out of all sites where the species was not detected. Concordance is a measure of the how often a site where a species was detected is assigned a higher $\hat{\psi}$ than a site where the species was not detected, thus, making it a measure of predictive strength that is independent of investigator-defined prediction cutoff criteria. Concordance values > 0.5 indicate that predictions made by a model are better than a random classification of observations, and values of 1.0 indicate that all sites where a species was detected had a higher predicted values of $\hat{\psi}$ than all sites where the species was not detected (Kutner et al. 2004).

Observed species occurrences at the 32 wetlands surveyed for amphibians in PA-DEWA served as a model validation data set. Model parameters used to predict occupancy states at surveyed NJ-DEWA sites were also used to predict occupancy states at surveyed PA-DEWA sites. Using the same criteria prediction cut-off value as in model training sites, accuracy measures of percent correct classification, sensitivity, specificity, and concordance were calculated for model validation sites.

We used correlation analyses to compare error rates between model training and validation data sets for each species to determine if there were consistent patterns in the type of errors that were being made (i.e., commission vs. omission errors). We also

looked at the relationships between error rates and values of \bar{p}^* for each species to assess whether sampling efficiency affected model prediction error.

RESULTS

Hydrology of Surveyed Wetlands

Of the 44 wetlands sampled for amphibians in NJ-DEWA, 10 were hydrologically isolated, 14 contained seasonal hydrologic connections, and 20 contained permanent hydrologic connections. Among these wetlands, hydrologically isolated wetlands ranged in size from 0.012 ha to 0.619 ha, seasonally connected wetlands ranged in size from 0.013 ha to 4.25 ha, and wetlands with permanent connections ranged in size from 0.024 ha to 6.06 ha. By the week of 12 June 2005, only 30% of these isolated wetlands ($n = 3$) contained standing water, and there was little correlation between their June drying score and their size during high water conditions (Pearson correlations: $r = -0.080$, $P = 0.826$). At that same time, nearly 70% ($n = 4$) of wetlands with seasonal connections contained standing water, and there was a weak correlation between their current drying score and size during high water conditions ($r = 0.415$, $P = 0.140$). Logistic regression suggested that the presence of standing water is better explained by hydrologic connectivity ($\beta = 1.85 \pm 0.96$, $P = 0.055$) than wetland size ($\beta = 1.01 \pm 0.832$, $P = 0.223$) among wetlands without permanent hydrologic connections. Accounting for wetland size, wetlands with seasonal hydrologic connections were 6.35 times more likely contain standing water in mid-June than isolated wetlands.

Probability of Detection and Sampling Efficiency

Final occupancy models indicated that the mean probability of detecting a species among all sites (\bar{p}^*) exceeded 95% for four species (*R. palustris*, *A. maculatum*, *R. sylvatica*, and *R. clamitans*), were 76 - 71% for three species, and were lowest for *R. catesbeiana* and *H. versicolor* (Table 1.2). Wetland size predicted detection probabilities of three species (*N. viridescens*, *Bufo*, and *P. crucifer*), fish presence predicted the detection probabilities of three species (*H. versicolor*, *R. catesbeiana*, and *R. sylvatica*), and the detection probabilities of two species (*A. maculatum* and *R. clamitans*) were predicted by models incorporating both wetland size and fish presence (Table 1.2). Detection

probabilities for *N. viridescens*, *P. crucifer*, *R. clamitans* increased with wetland size, but size had a less dramatic effect on detection probability of *R. clamitans* in wetlands that contained fish than in wetlands that did not. In contrast, wetland size was modeled as having a negative effect on the detection of *Bufo* species and *A. maculatum*, although the error surrounding its regression coefficient suggests this is not a statistically significant relationship in *A. maculatum*. The presence of fish made it more difficult to detect *A. maculatum*, *H. versicolor* and *R. sylvatica*, although fish presence was not a significant predictor for *A. maculatum*. Detectability was shown to have a positive relationship with fish presence for *R. catesbeiana*. There were no significant predictor variables for the detection of *R. palustris*, and *Bufo* was the only species to be modeled with a constant detection probability over all survey events.

Modeling Occupancy

Wetland size and connectivity were the most important predictors of occupancy for amphibian species in NJ-DEWA with either one or both parameters included in the final occupancy models for five of the nine amphibian species. Forest canopy cover played an important role in predicting occupancy for five species and spatial isolation was important for only one species (Table 1.3).

Hydrologic connectivity was positively related to occurrence for *R. clamitans* and *R. catesbeiana*. Larvae of both of these species over-winter in wetlands, and their odds of occurrence were approximately 10 and 8 times higher, respectively, in wetlands with permanent hydrologic connections than those with seasonal connections. Furthermore, the odds of occurrence for *R. clamitans* and *R. catesbeiana* were approximately 105 and 61 times lower, respectively, in isolated wetlands than wetlands with permanent connections. Occupancy by *R. clamitans* was dependent upon both wetland size and connectivity in an additive matter, but only connectivity was found to be a significant predictor of *R. catesbeiana* occurrence. Hydrologic connectivity was negatively related to occupancy for *R. sylvatica*. Wetlands with permanent hydrologic connections were 8.6 times less likely to contain *R. sylvatica* than wetlands with either isolated wetlands or

those with seasonal connections. After accounting for hydrologic connectivity, no other predictor variable was related to the probability of occupancy for *R. sylvatica*.

Wetland size displayed a positive relationship with occupancy for four species, and was always accompanied by other predictor variables in best-fit occupancy models. Occupancy increased with wetland size in an additive fashion with the percent of forest canopy cover at the 250 m scale for *A. maculatum* (Figure 1.1), and with hydrologic connectivity for *R. clamitans* (Figure 1.2). For these species, the odds of occupancy increase 6.3 and 7.4 times, respectively, as wetland size increased by an order of magnitude. In contrast, it was the interaction between wetland size and hydrologic connectivity that was important in explaining occupancy for both *P. crucifer* (Figure 1.2) and *R. palustris* (Figure 1.3). For both species, occupancy increased sharply with wetland size in isolated wetlands, increased less so in wetlands with seasonal connections, and remained relatively unchanged in wetlands with permanent connections. As size increased by an order of magnitude, the odds of *P. crucifer* occurring in isolated wetlands increased 645-fold, whereas in wetlands with seasonal connections it increased only 21-fold. Occupancy probabilities of *P. crucifer* in isolated wetlands would exceed those of seasonally connected wetlands only in sizes that exceed 0.5 ha. For *R. palustris*, as size increases by an order of magnitude, the odds of occurrence increased over 1,600-fold in isolated wetlands, and 60-fold in wetlands with seasonal connections. In wetlands that exceed 1.5 ha, the probability of occupancy was predicted to be higher in isolated wetlands than seasonally connected wetlands. However, observations for isolated wetlands that exceed 0.62 ha in size were limited, so inferences are suspect.

The presence of both salamander species, *A. maculatum* and *N. viridescens*, were positively associated with the percent of forest canopy cover at the 250m scale (Figures 1.1 and 1.4). The odds of occurrence for these species in wetlands with 100% closed canopy were 18 and 460 times higher, respectively, than the odds of occurrence in wetlands with 50% closed canopy at the 250m scale. *Rana palustris* was the only anuran species whose presence was negatively influenced by canopy cover at the 250m scale, and it was 676 times less likely to occur in wetlands with 100% closed canopy than

wetlands with 50% closed canopy. Percent canopy cover at the 25m scale exhibited a negative effect on occupancy for three species; *N. viridescens* (Figure 1.4), *Bufo* species, and *H. versicolor* (Figure 1.5). Although canopy cover at the 250 m and 25 m scale influenced *N. viridescens* occupancy in an opposite manner, the magnitude of their influences were equivalent as reflected in the values of their regression coefficients. As a predictor variable for *Bufo* occupancy, canopy cover at the 25 m scale displayed a relatively large amount of variation and was not considered a significant predictor of occupancy ($p > 0.05$ level), even though AIC criteria deemed this model to have considerably more empirical support than a null model for occupancy. Both canopy cover at 25 m and the number of wetlands within 1km (i.e., spatial isolation) were significant predictors of *H. versicolor* occupancy, with canopy cover exerting a relatively strong influence on occupancy. Wetlands that have 100% covered canopy are not predicted to have *H. versicolor* unless they have at least 13 wetlands within 1 km. Only five potential breeding wetlands in NJ-DEWA with 100% canopy cover fit this criterion for spatial isolation.

Best fit models of *A. maculatum*, *N. viridescens*, and *H. versicolor* were not improved by adding fish presence as a covariate of occupancy (AIC scores increased), and fish presence was not considered a significant predictor of occupancy for any of these species (Table 1.4). Similarly, substituting the predictor variable FISH for CONNECT in best fit models of *P. crucifer*, *R. catesbeiana*, *R. clamitans*, and *R. palustris* did not result in lower AIC scores, but it did for *R. sylvatica*. In comparing AIC scores, a fish presence model of *R. sylvatica* occurrence was significantly better than a hydrological connectivity model, and *R. sylvatica* was 14.5 times more likely to occur in fishless wetlands than those that contained fish. Although the connectivity-based model for *R. clamitans* occurrence provided a significantly better fit than a fish presence-based model, *R. clamitans* were predicted to be 7.6 times less likely to occur in fishless wetlands than wetlands that contain fish. We could not assess the importance of fish presence in *Bufo* occupancy models because the inclusion of the variable FISH in models prevented numerical convergence of maximum likelihood estimates.

Occupancy models for fish presence suggest the probability of detecting fish remained constant between survey periods, and detectability increased with wetland size (Table 1.2). The mean probability of detecting fish (\bar{p}^*) among all sites was 88.5%, but among sites with permanent hydroperiods $\bar{p}^* = 95.2\%$. The presence of fish at sites was positively related to hydrologic connectivity (Table 1.3) and fish had a 64.6% chance of occupying wetlands with permanent hydrologic connections. Fish were four times less likely to occur in wetlands with seasonal hydrologic connections ($\hat{\psi} = 31.1\%$), and only had a 10% probability of occupying hydrologically isolated wetlands. The addition of wetland size to models with hydrologic connectivity did not improve model fit (AIC scores increased), and wetland size was not a significant predictor of occupancy in models that did not include hydrologic connectivity ($\beta_{\text{Size}} = 0.686 \pm 0.479$).

Model Validation and Accuracy

The percent of sites with correctly classified occupancy states averaged 79.8% among species for training data, and averaged 72.9% for validation data (Table 1.5). Mean sensitivity and concordance scores among species was higher for training data sets (85.8% and 88.7%, respectively) than validation data sets (sensitivity = 57.8%, concordance = 73.7%). Mean specificity scores, in contrast, were slightly higher for validation data sets than for training data sets. Models that performed poorly at predicting occupancy (%Correct) and well at predicting absences (specificity) with training data tended to perform poorly with validation data (Pearson correlations: %Correct: $r = 0.720$, $P = 0.029$; Specificity: $r = 0.578$, $P = 0.101$). Mean species detection rates (\bar{p}^*) were not correlated with model accuracy at training data sites, but were correlated with two measures of model accuracy at validation sites. Detection rates displayed a negative association with the accuracy of predicting absence at validation sites (Specificity: $r = -0.674$, $P = 0.046$) and displayed a positive association with the accuracy of predicting presence at validation sites (Sensitivity: $r = 0.804$, $P = 0.009$). Sensitivity exceeded specificity for 7 species in training data, whereas specificity exceeded sensitivity for 7 species among validation data sets.

Rana palustris models performed exceptionally well for both model training and model validation data sets. Notably, at validation sites, *R. palustris* models correctly classified occupancy states at 90% of sites, and 99% of the time it predicted higher occupancy probabilities at sites that contained *R. palustris* than at sites that did not (i.e., concordance score). The *Bufo* model, despite performing poorly at predicting presence at occupied sites (i.e., sensitivity), performed well at validation sites by correctly predicting occupancy 86.4% of the time, and predicting higher occupancy probabilities for occupied sites than unoccupied sites over 85% of the time (i.e. concordance score). The *A. maculatum* model appeared to over-predict presence (as reflected in low specificity scores), but, like *Bufo*, overall correct classification rates and concordance scores were relatively high among both training and validation sites.

Models for *R. sylvatica* and *H. versicolor* were the least accurate of all species for both training and validation data sets (Table 1.5). In validation data sets, the *R. sylvatica* model tended to predict presence at sites where the species was not detected, whereas *H. versicolor* model errors tended to predict absence at sites where the species was detected. In addition, low concordance scores at validation sites for these species indicate that predicted presence probabilities were similar between sites where the species was detected and those where they were not detected. This suggests that model prediction error rates would not improve if alternative probability cut-off criteria were used (e.g., using an occurrence cutoff based on the proportion of sites occupied rather than >0.50).

DISCUSSION

Amphibian Occupancy Models and Model Validation

Hydrologic characteristics of wetlands played an important role in determining species presence for two-thirds of the species studied. Hydrologic connectivity was important in predicting the occurrence of five out of nine species, and it was the sole predictor variable for two of those species. Permanent hydrologic connections had a negative effect on occurrence for the early spring breeding species *R. sylvatica*, a positive effect on occurrence for the summer breeding species *R. clamitans* and *R. catesbeiana*, and displayed an interaction with wetland size for the spring breeding species *P. crucifer* and

R. palustris. In DEWA, *R. sylvatica* is often the first amphibian species to initiate metamorphosis: previous work in DEWA suggested the negative effect of fish presence on *R. sylvatica* egg mass abundance was considerably stronger than the positive effect of a stable seasonal hydroperiod (Julian et al. 2006). In this study, we found that hydrologic connectivity, but not wetland area, was a significant predictor of fish presence. Thus, for *R. sylvatica*, wetlands with permanent hydrologic connections represented habitats where the risk of predation outweighed the benefit of a permanent hydroperiod.

In contrast, *Rana clamitans* and *R. catesbeiana* have larvae that remain in the larval stage for at least one year, therefore, they must rely on wetlands with permanent and semi-permanent hydroperiods. These species are unpalatable to many fish species (Kats et al. 1988), and fish may reduce populations of invertebrate predators that consume their larvae (Werner and McPeck 1994, Smith et al. 1999). Furthermore, *R. catesbeiana* can be more likely to occur, and persist, in ponds when fish are present (Maret et al. 2006). *Rana catesbeiana* occurrence was best predicted by connectivity alone, whereas that of *R. clamitans* was predicted by the additive effects of connectivity and size because *R. catesbeiana* larvae overwinter at least twice, and they would be less successful at using semi-permanent ponds than *R. clamitans* whose larvae over-winter only once.

For *P. crucifer* and *R. palustris*, the probability of occupancy in wetlands with permanent connections is relatively fixed across a wide range of sizes, whereas the probability of occupancy increased with size at a faster rate in hydrologically isolated wetlands than in wetlands with seasonal hydrologic connections. In wetlands with permanent connections there is no threat of pond drying, and predator assemblages would be expected to be similar across wetland sizes if presence for other predators follow trends for fish. In contrast, the threat of drying is higher in isolated than seasonally-connected wetlands. Therefore, wetlands with seasonal connections would be expected to have higher occupancy rates than isolated wetlands until they reach a size that is indicative of an isolated wetland where the threat of drying is minimal and the threat of predation is increased. This hypothesis is consistent with the prediction that a higher occupancy rate in isolated wetlands occurs at a smaller wetland size for *P. crucifer* than *R. palustris*

because the larvae of *P. crucifer* metamorphose approximately 1 month earlier than *R. palustris*.

Wetland size was important in predicting the occurrence of four species, but it differed from hydrologic connectivity because it displayed only positive relationships with species occupancy, and it was always necessary to place wetland size in the context of other covariates such as hydrologic connectivity (for *P. crucifer*, *R. clamitans*, and *R. palustris*) or forest canopy cover within 250 m (for *A. maculatum*) to best model occupancy. A number of studies have found that wetland size is not correlated with amphibian species richness (Hecnar and M'Closkey 1996, Lehtinen and Galatowitsch 2000, Snodgrass et al. 2000, Weyrauch and Grubb 2004), and we have observed these studies either fail to consider hydrologic connectivity as predictor, or include wetlands that do not vary substantially with respect to hydrologic connectivity. Occupancy rates of species that are highly susceptible to predation could conceivably decrease with increasing wetland size if size correlates with the occurrence, abundance, or diversity of aquatic predators such as fish, dragonflies, Phryganeid caddis flies, Belostomatid water bugs, and Dytiscid beetles, however, we did not attempt to model amphibian occurrence based on these taxonomic groups or predator diversity.

The occurrence of five species was predicted, in part, by landscape-level variables. Proportion of forest canopy cover at the 250 m scale was positively associated with the occurrence of both salamander species. Forest canopy cover at the 250 m scale was negatively associated with *R. palustris* occurrence, even though forest canopy cover at large spatial scales ($\geq 250\text{m}$) has repeatedly been shown to predict species presence (Guerry and Hunter 2002, Porej et al. 2004, Rubbo and Kiesecker 2005) and species richness for amphibian communities (Findlay and Houlihan 1997, Hecnar and M'Closky 1998, Knutson et al. 1999, Rubbo and Kiesecker 2005). The adult and juvenile stages of *Ambystoma* species occupy forested upland habitats that provide protection against desiccation during seasonal migrations and during the non-breeding season (Rothermel and Semlitsch 2002), whereas *N. viridescens* relies heavily on forested uplands during its juvenile stage that lasts as long as 3 years, and when adults foray into forested areas

immediately surrounding ponds during the summer months. Forest canopy at the 250 m scale did not predict *R. sylvatica* occurrence, but we suspect this scale may not have been large enough. Dispersal ranges for migrating amphibian species can be grossly underestimated, and dispersal distances can exceed 400 m for *A. maculatum* (Montieth and Paton 2006), and 1 km for *A. opacum* (Gamble et al. 2006) and *R. sylvatica* (Calhoun and deMaynadier 2004). Porej et al. (2004) found a positive relationship between *R. sylvatica* occurrence and % forest canopy within 200 m of ponds, but concluded it could be difficult to identify canopy cover thresholds for this species in light of its dependency on forest cover at larger spatial scales. Furthermore, there is a considerable amount of forested habitat in DEWA, and the minimum threshold of canopy cover required to elicit a response in *R. sylvatica* occurrence may not have been approached. This is supported by Homan et al. (2004) that predicted this threshold at the 300 m scale would occur when 55% of the area is classified as a forested cover-type.

Proportion of closed forest canopy at the 25m scale was found to have a negative effect on occurrence for three species, *N. viridescens*, *Bufo sp.*, and *H. versicolor*. Solar radiation is greater in ponds with less riparian canopy cover, and increased solar radiation increases water temperatures, *in situ* primary productivity, and dissolved oxygen concentrations (Skelly et al. 2002). Sjorgen (1995) found that water temperature and solar radiation increased the probability of occurrence for the pool frog (*Rana temporaria*) and Burne and Griffin (2005a) found that in-pond tree canopy coverage had a negative relationship with amphibian species richness in the study area in eastern Massachusetts. The interplay between solar radiation and forest canopy has also been shown to directly impact amphibian larvae. Werner and Glennemeir (1999) found that larval survival and growth were depressed for *Bufo americanus* and *Rana pipiens* in closed canopy ponds, and concluded this disparity was due to limited food resources in closed-canopy ponds. However, larval growth and survival of the closed canopy species, *R. sylvatica*, was not compromised when raising these tadpoles in open-canopy ponds. Skelly et al. (2002) found strong evidence that food limitation significantly reduced growth rates of both *P. crucifer* and *R. sylvatica* in closed canopy, as opposed to open canopy, ponds. In addition, common garden experiments by Skelly et al. (2002) suggested *R. sylvatica*

growth was less impacted by some closed-canopy conditions. Furthermore, evapotranspiration is a major contributor to water loss in vernal pools (Brooks 2004), so we can expect shorter hydroperiods in wetlands with more forest canopy cover in their immediate riparian zone.

Even though spatial isolation often predicts amphibian species occurrence (Vos and Stumpel 1996, Vos and Chardon 1998) and species richness (Hecnar and M'Closkey 1998, Lehtinen et al. 1999, Burne and Griffin 2005a), *H. versicolor* was the only species in DEWA whose occurrence appeared to be affected by spatial isolation. Metapopulation theory would predict that amphibian breeding wetlands within close proximity to adjacent breeding wetlands would have a higher probability of being occupied than those that are more spatially isolated. This trend, however, may not be as strong in relatively undisturbed habitats (like NJ-DEWA) as it would be in highly fragmented landscapes (Marsh and Trenham 2001), and we have yet to explore relationships between spatial isolation and other metapopulation parameters such as multi-season extinction/colonization rates. We expected spatial isolation to affect occupancy rates of *N. viridescens*, *R. sylvatica*, and *A. maculatum* because populations of these species have been characterized as exhibiting metapopulation dynamics. If occurrences of these species are influenced by spatial isolation, we may have failed to detect these relationships because we used inappropriate isolation metrics or quantified metrics at an inappropriate scale. We examined occupancy relationships with both distance-based (nearest-neighbor distance) and density based (wetlands /km and wetlands area/km) isolation metrics that have previously been associated with amphibian species richness and occurrence. Other measures such as inverse distance weighted measures and cost-path analysis (Ray et al. 2002) have also proven insightful in amphibian studies. However, isolation metrics are notoriously correlative, and these alternative measures would not necessarily shed additional light on occupancy patterns. Although the above approaches treat the “value” of adjacent ponds as either equal, a function of their size, or a function of their proximity, none of them account for the quality of adjacent wetlands when quantifying spatial isolation. One approach that attempts to measure spatial isolation in the context of the quality of adjacent wetlands is autologistic regression

(Augustin et al. 1996), although we are unaware of any attempts to incorporate this approach into the framework of occupancy modeling.

Occupancy models developed with training data from NJ-DEWA sites estimated robust empirical relationships that accurately predicted species occurrences at model validation sites in PA-DEWA. This is important because predictor variables used in occupancy models can be easily assessed at wetland habitats, and model validation sites occurred in a landscape that differed from model training sites in topographic features (namely aspect), and human development pressure (namely, higher road densities and a more urbanized landscape in PA-DEWA). Occupancy models developed for amphibian assemblages in DEWA provided relatively accurate predictions of species occurrences compared to models found in the Ornithological literature. Klute et al. (2002) predicted occurrences of woodcock in the Ridge and Valley province of Pennsylvania using logistic regression and spatially-explicit autologistic regression models that correctly predicted occupancy states at 62.4%, and 81.6% of model training sites, respectively. Shiner et al. (2002) produced logistic regression models to predict wood thrush occurrence in the Great Smokey Mountains that resulted in correct classification rates of 83.0% for training, and 86.0% for validation sites. Concordance scores for their training sites (77.9%) were lower than those from every species in NJ-DEWA, whereas the concordance score for their validation sites (78.9%) was equivalent to the mean concordance score of validation sites from all PA-DEWA species. Hepinstall et al. (2002) examined correct classification rates for GAP analysis and Bayesian models developed for 29 bird species and found that rates never exceeded 78% for training sites, or 73% for validation sites. Validation sets for six PA-DEWA species had higher correct classification rates than the best logistic regression, Mahalanobis distance, and Discriminant Function Analysis models that Dettmers et al. (2002) produced for two validation data sets for each of six bird species. Dettmers et al. (2002) was able to produce CART models that predicted species presence for black-throated green warblers with correct classification rates of 92% and 94.9%, but the mean correct classification rate for all of their CART models (66.0%) was lower than the mean rate from our nine PA-DEWA species (72.9%).

We feel that occupancy models developed for DEWA amphibian species performed as well, if not better, than models developed in previous studies of amphibians. Kolozvary and Swihart (1999) used logistic regression to develop predictive models for terrestrial and aquatic stages of nine amphibian species distributed among patches of forest in west-central Indiana. In that study, Somer's D (number of concordant pairs minus the number of discordant pairs, divided by the total number of pairs) was used to evaluate the accuracy of their training data, and these values ranged among species from 49.8% to 92.9%. The range of Somer's D scores for DEWA training sets were similar (61.8% to 92.0%), and 60.5% of all complete pairwise comparisons of Somer's D scores were higher for DEWA species than for species models from Kolozvary and Swihart (1999). Suzuki et al. (2008) developed logistic regression models for the Siskiyou Mountains Salamander using landscape level data at a variety of spatial scales. These models were less accurate than all species models in DEWA, with correct classification rates of validation sites never exceeding 70% for any model.

We accounted for the effects of wetland size and fish presence on our ability to detect each species by using occupancy models. This was an important strategy because our sampling effort was proportional to wetland size, and aquatic predators have been shown to cause amphibian larvae to become less conspicuous in the water column (Holomuzki 1986, Petranka et al. 1987, Semlitsch 1987, Stangel and Semlitsch 1987, Kiesecker and Blaustein 1998). Occupancy models suggest that among validation sites, poorly sampled species (those with low \bar{p}^* estimates) were associated with low sensitivity scores, and thoroughly sampled species were associated with low specificity scores. This could mean either the probability cutoff values were too high, or models underestimate $\hat{\psi}$ for poorly sampled species and over estimate $\hat{\psi}$ for thoroughly sampled species. In training and validation data sets, *A. maculatum*, *Bufo*, and *R. palustris* models predicted species occupancy with relatively high accuracy, whereas *R. sylvatica* and *H. versicolor* models predicted occupancy with relatively low accuracy. The relative accuracy of species models were consistent between model training and validation data sets for correct classification rates and specificity scores, but not for concordance and sensitivity scores.

Management Recommendations for Assessing Hydrologic Connectivity

In developing management plans for pond-breeding amphibians, we recommend that resource managers characterize hydrologic connectivity at all potential amphibian breeding wetlands because hydrologic connectivity is a significant predictor of amphibian species occurrence that is correlated with, yet easier to assess, than proximal factors that shape amphibian assemblages such as fish presence and seasonal hydroperiod. We conclude that hydrologic connectivity provides relatively more “information” to occupancy models than fish presence because neither the addition of fish presence as a predictor variable to final models, nor its substitution for hydrologic connectivity, produced better-fit models for predicting amphibian species presence (with the exception of *R. sylvatica*). These results were surprising because fish presence has been repeatedly shown to have a negative effect on both amphibian species presence (Kats and Sih 1992, Hopey and Petranka 1994, Knapp and Matthews 2000, Julian et al. 2006) and species richness (Hecnar and M’Closkey 1998), and fish can influence inter-specific competitive outcomes between amphibian larvae (Morin 1983). Our results suggest the impact of fish on amphibian populations should be evaluated in the context of additional parameters related to hydrologic connectivity such as hydroperiod, other predatory species, or water chemistry.

Hydrologic connectivity is highly informative in predicting amphibian occurrence because it represents ordinal information that can confer desiccation risk, predator diversity and abundance, and water chemistry parameters. Wetlands with seasonal connections are much less likely to dry than isolated wetlands, and the linkage between longer hydroperiods and the increased abundance and diversity of predatory species is quite clear from the literature. Furthermore, seasonal connections could allow for re-colonization of semi-permanent ponds by fish and other predators. Extensive research on montane ponds in the Sierra-Nevada range has linked the decline of native amphibian fauna to the introduction and establishment of non-native trout in networks of streams that connect breeding wetlands (Bradford et al. 1993, Knapp and Matthews 2000, Vredenburg 2004). Wetlands with more permanent hydrologic connections could also

signify strong ground-water contributions to wetlands that influence water chemistry parameters such as pH, conductivity, ion concentrations, and turbidity that have been associated with amphibian species occurrence (Clark 1985, Rowe and Dunson 1993, Horne and Dunson 1994).

Hydrologic connectivity can be easily assessed in the field with a single site visit to ponds under summer, “low-water” conditions because dried canals can be identified by slight topographic draws/depressions, stained leaf-litter, paths of scoured vegetation, and/or discontinuities in vegetations. Even in years when excessive rainfall prevents typically ephemeral ponds from drying, investigators would still be able to discriminate isolated from non-isolated wetlands. Under such conditions, some seasonal hydrologic connections could be falsely classified as permanent connections, but these errors would also occur if pond hydroperiods were being assessed. It is unlikely that a single site visit would result in an accurate assessment of fish presence because of the likelihood that individuals may go undetected. When we modeled fish detection as a function of wetland size, the mean probability of detecting fish at one of our sites during a given visit was approximately 52.4% (same p for a wetland approximately 0.25 ha in size). Therefore, to detect fish presence with 95% certainty investigators would have to visit the average site approximately four times during the year.

In contrast to fish occurrence or wetland hydroperiod, hydrologic connectivity could also be assessed remotely using available hydrologic and topographic GIS datalayers. Organized in a GIS, investigators could categorize potential breeding wetlands by their adjacency to digitized stream information available through NWI, or the U.S. Geological Survey digital line graphs (DLG) or digital raster graphs (DRG) hydrologic datalayers. If these streams are attributed with hydrological modifiers (Cowardin et al. 1976) that characterize hydroperiod, this information could be used to classify hydrologic connectivity on an ordinal scale of the investigator’s choice. This approach was used by Tiner (2003b) to assess the abundance of hydrologically isolated wetlands from among 72 study areas across the conterminous United States. Furthermore, digital elevation maps (DEM) could be used to identify topographic features that signify seasonal

hydrologic connections such as small drainage channels or draws that intersect wetlands. Such features could be detected using DEMs produced by airborne sensor arrays such as light detecting and ranging (LiDAR) that produce fine-scale, sub-meter measurements of elevation.

An assessment of hydrologic connectivity is necessary to categorize wetlands under classification schemes such as the Hydro-Geomorphic Model (HGM) system that consider hydrologic connectivity, landscape position, and likely water source when classifying a wetland (Brinson 1993). Such schemes are based on easily assessable abiotic factors that place wetlands within a classification that has been shown to have predictable ecological/biotic associations and, to some extent, wetland hydroperiod (Cole et al. 1997, Cole and Brooks 2000). Furthermore, proposed modifications to the HGM system include consideration of the seasonality of hydrologic connections, and our research illustrates the biotic implications of such seasonality.

The designation of a wetland as hydrologically isolated in a legislative context has fundamental implications to its designation as a protected body of water on the national, and sometimes state, and local levels. The United States Supreme Court decision in *Solid Waste Agency of Northern Cook County vs U.S. Army Corps of Engineers* reduced the legal protection of hydrologically isolated wetlands afforded by the *Clean Water Act* by limiting the Act's protection to "wetlands that are adjacent to, tributaries of, or display a significant nexus to a navigable body of water". In the Court's decision in *Rapanos vs U.S. Army Corps of Engineers*, the Court placed the onus on federal agencies (i.e. the U.S. Environmental Protection Agency and U.S. Army Corps of Engineers) to establish guidelines on which seasonal hydrologic connections constitute a tributary or a significant nexus to a navigable body of water. There is a growing list of state and local municipalities that have enacted legislation that specifically protects wetlands that are hydrologically isolated, but none protect the entire 250m buffer-area of critical upland habitat required by vernal-pool breeding amphibians (Mahaney and Klemens 2008). Our study illustrates the importance of characterizing the size and hydrologic connectivity of these wetlands to predict the occurrence of amphibians that can subsequently be used to

prioritize upland habitats of with high conservation value that require non-legislative protection such as public or non-governmental agency acquisition or easement.

Table 1.1. Number of NJ-DEWA wetlands surveyed in 2005 according to wetland size and geographic isolation classes.

		Geographic Isolation Class		
		0-3 ponds	4-7 ponds	≥ 8 ponds
Size	< 0.1 ha	6	6	4
	0.1 – 0.66 ha	4	4	7
	≥ 1 ha	4	6	3

Table 1.2. Summary of detection probability (p) regression coefficients ($\beta \pm 1SE$) and mean cumulative detection probabilities (\bar{p}^*) for final occupancy models of nine amphibian species and predatory fish sampled in the DEWA in 2005.

Species	Regression coefficients for p ($\pm 1 SE$)			\bar{p}^* all sites surveyed
	AREA ¹	FISH ²	FISHXAREA ³	
<i>A. maculatum</i>	-0.304 ± 0.243	-0.718 ± 0.400		0.999
<i>N. viridescens</i>	1.369 ± 0.461			0.712
<i>Bufo</i> species	-1.963 ± 0.826			0.714
<i>H. versicolor</i>		-2.925 ± 1.181		0.535
<i>P. crucifer</i>	0.954 ± 0.370			0.757
<i>R. catesbeiana</i>		1.520 ± 0.687		0.658
<i>R. clamitans</i>	1.352 ± 0.454	3.068 ± 1.910	-1.142 ± 0.548	0.982
<i>R. palustris</i>				0.952
<i>R. sylvatica</i>		-1.632 ± 0.605		0.993
Fish presence	1.352 ± 0.336			0.884

¹AREA: wetland area

²FISH: fish present=1, fish not present=0

³FISHXAREA: interaction term between SIZE and FISH

Table 1.3. Summary of regression coefficients ($\beta \pm 1$ SE) for probability of occupancy ($\hat{\psi}$) from final occupancy models for 9 amphibian species sampled in the DEWA in 2005.

Species	AREA ¹	CONNECT ²	AREAX CONNECT ³	P250 ⁴	P25 ⁵	PONDS 1KM ⁶
<i>A. maculatum</i>	1.88 ±0.92			3.71 ±1.79		
<i>N. viridescens</i>				7.80 ±3.45	-7.95 ±2.86	
<i>Bufo</i> species					-7.87 ±4.12	
<i>H. versicolor</i>					-11.09 ±4.99	1.04 ±0.52
<i>P. crucifer</i>	9.36 ±1.11	11.94 ±1.60	-3.15 ±0.39			
<i>R. catesbeiana</i>		2.05 ±0.95				
<i>R. clamitans</i>	1.96 ±0.92	2.34 ±0.78				
<i>R. palustris</i>	10.85 ±0.67	13.80 ±0.94	-3.34 ±0.20	-8.29 ±2.86		
<i>R. sylvatica</i>		-2.15 ±0.79				
Fish presence		1.40 ±0.56				

¹AREA: wetland area

²CONNECT: strictly isolated=1, seasonal connection=2, permanent connection=3

³AREA X CONNECT: interaction term between SIZE and CONNECT

⁴P250: proportion of forested area within 250 m of flooded perimeter with > 50% canopy cover

⁵P25: proportion of forested area within 25 m of flooded perimeter with > 50% canopy cover

⁶PONDS1KM: number of amphibian breeding wetlands within 1 km of flooded perimeter

Table 1.4. Summary of regression coefficients ($\beta \pm 1$ SE) for probability of occupancy (ψ) from occupancy models that incorporate fish presence, but not hydrologic connectivity for wetlands in the DEWA in 2005.

Species	Δ AIC from final model	$\hat{\psi}$ covariate with regression coefficient				
		AREA ¹	FISH ²	P250 ³	P25 ⁴	PONDS 1KM ⁵
<i>A. maculatum</i>	+1.58	1.93 ±6.85	-0.66 ±1.52	3.24 ±2.46		
<i>N. viridescens</i>	+2.00		-0.080 ±1.44	7.76 ±3.51	-7.98 ±2.92	
<i>H. versicolor</i>	+1.19		-1.88 ±2.12		-12.6 ±5.7	1.03 ±0.53
<i>P. crucifer</i>	+5.91	1.17 ±0.63	0.16 ±0.88			
<i>R. catesbeiana</i>	+4.21		1.49 ±1.08			
<i>R. clamitans</i>	+9.58	2.00 ±0.72	1.99 ±0.95			
<i>R. palustris</i>	+6.14	1.74 ±0.71	1.52 ±0.99	-4.70 ±2.49		
<i>R. sylvatica</i>	-4.83		-2.67 ±0.78			

¹AREA: wetland area

²FISH: fish present=1, fish not present=0

³P250: proportion of forested area within 250 m of flooded perimeter with > 50% canopy cover

⁴P25: proportion of forested area within 25 m of flooded perimeter with > 50% canopy cover

⁵PONDS1KM: number of amphibian breeding wetlands within 1 km of flooded perimeter

Table 1.5. Accuracy measures of occupancy model predictions for model training (Train) and validation (Valid) data sets for amphibians in the DEWA in 2005.

Species	$\hat{\psi}$ covariates	%Correct	Sensitivity	Specificity	%Concord
		Train/ Valid	Train/Valid	Train/Valid	Train/Valid
<i>A. maculatum</i> *	Size, P250	86.3 / 75.0	100.0 / 95.2	25.0 / 30.0	89.0 / 80.5
<i>N. viridescens</i>	P25, P250	75.0 / 62.5	89.5 / 28.6	64.0 / 72.0	88.4 / 62.8
<i>Bufo species</i>	P25	86.4 / 84.4	71.4 / 50.0	89.2 / 92.6	86.9 / 86.7
<i>H. versicolor</i>	P25, Ponds1k	72.7 / 65.6	90.0 / 35.7	67.6 / 88.9	81.5 / 58.7
<i>P. crucifer</i>	SizeXConnect	77.3 / 68.8	90.0 / 52.9	66.7 / 86.7	86.9 / 71.8
<i>R. catesbeiana</i>	Connect	79.5 / 84.4	86.7 / 50.0	75.9 / 92.3	96.0 / 78.0
<i>R. clamitans</i> *	Size, Connect	81.8 / 62.5	84.6 / 46.7	77.8 / 76.5	94.4 / 68.6
<i>R. palustris</i> *	SizeXConnect, P250	86.4 / 90.6	88.9 / 75.0	84.6 / 95.8	95.3 / 99.0
<i>R. sylvatica</i> *	Connect	72.7 / 62.5	71.4 / 85.7	75.0 / 18.0	88.0 / 57.0
Averages		79.8 / 72.9	85.8 / 57.8	69.5 / 72.6	88.7 / 73.7

Species with $\bar{p}^ > 95\%$ for training data sets ($\bar{p}^* > 90\%$ in validation data sets for all species)

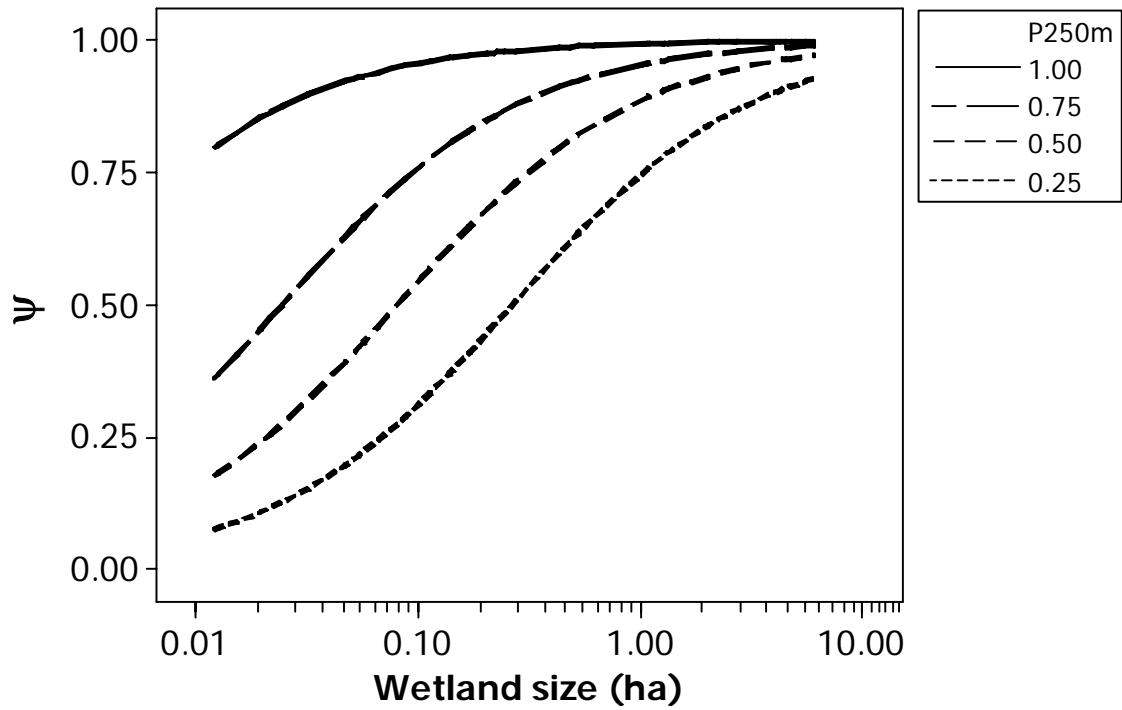


Figure 1.1. Probability of occupancy (ψ) for *A. maculatum* as a function of wetland size and proportion of forest canopy cover at the 250 m scale (P250m).

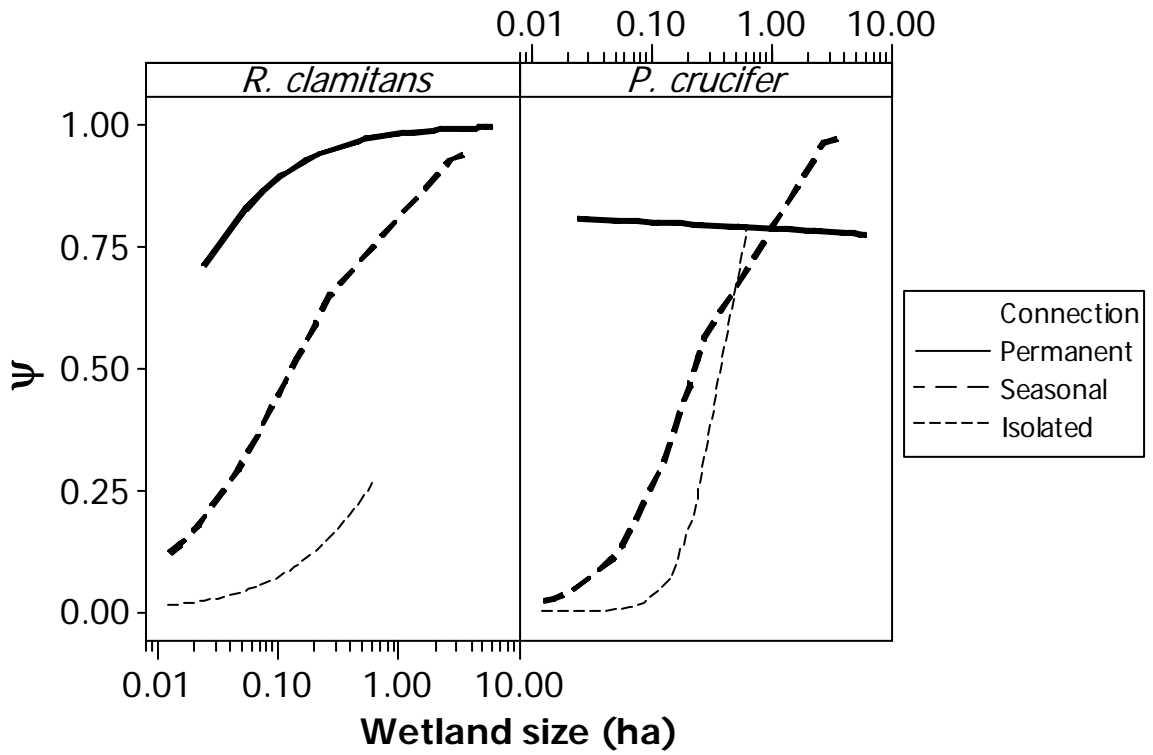


Figure 1.2. Probability of occupancy (ψ) for *R. clamitans* and *P. crucifer* as a function of wetland size and hydrologic connectivity.

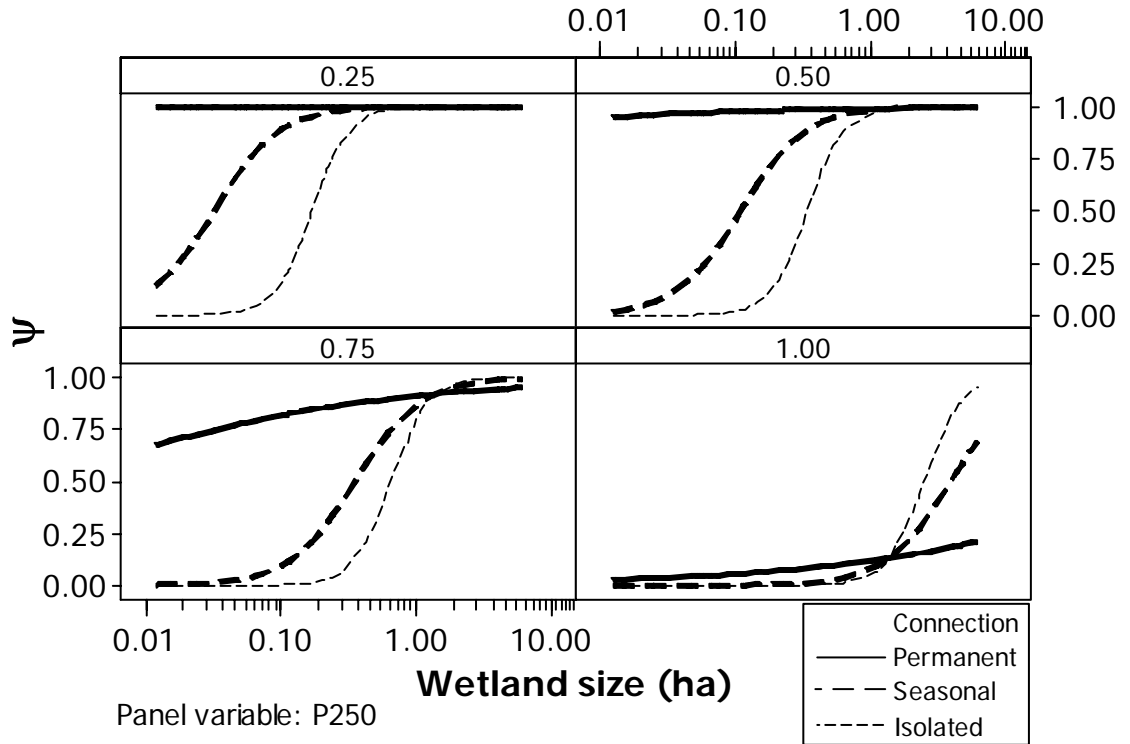


Figure 1.3. Probability of occupancy (ψ) for *R. palustris* as a function of wetland size, hydrologic connectivity (Connection), and proportion of forest canopy cover at the 250 m scale (P250).

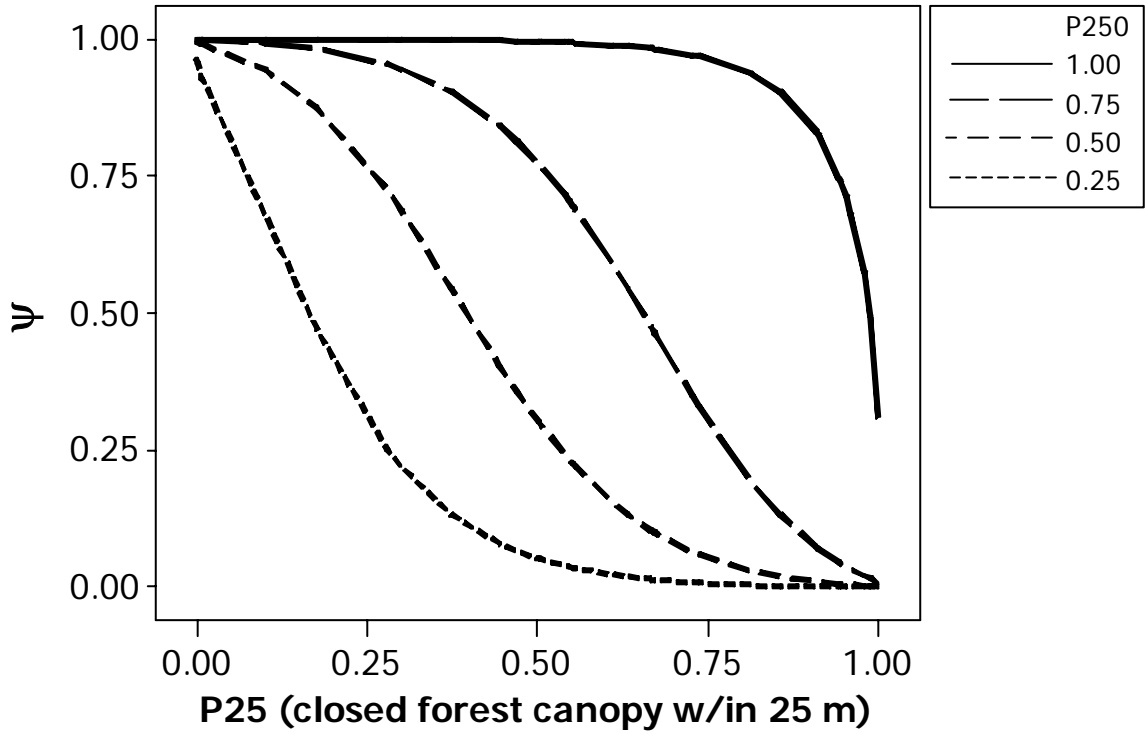


Figure 1.4. Probability of occupancy (ψ) for *N. viridescens* as a function of proportion of closed forest canopy with 250 m (P250) and 25 m (P25) of pond boundary.

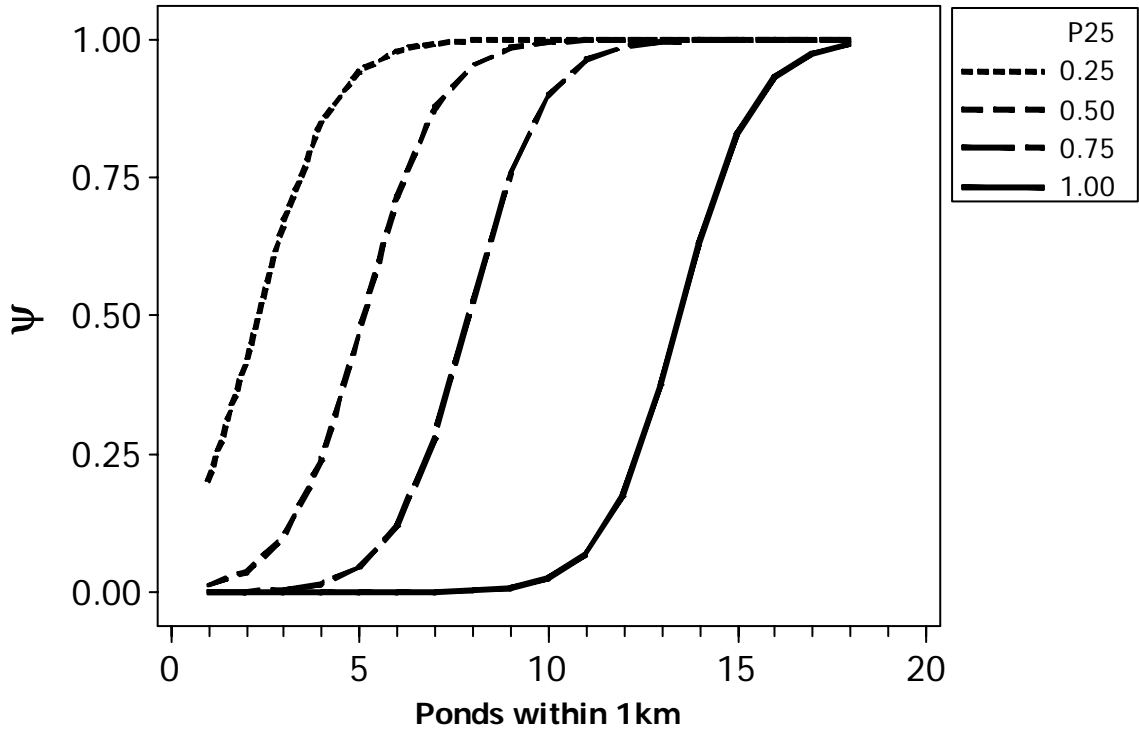


Figure 1.5. Probability of occupancy (ψ) for *H. versicolor* as a function of proportion of closed forest canopy within 25 m (P25) and the number of potential breeding wetlands within 1km.

CHAPTER 2:

The importance of small and hydrologically isolated wetlands to pond-breeding amphibians in Delaware Water Gap National Recreation Area

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ABSTRACT

Federal wetlands legislation typically protects only large wetlands, and those with permanent stream connections. As a result, this legislation can fail to protect a number of amphibian species that use small and hydrologically isolated wetlands as critical breeding habitats. We predicted the occurrence of nine pond-breeding amphibian species at 175 wetlands in the New Jersey portion of the Delaware Water Gap National Recreation Area based on amphibian surveys conducted in 2005, and tracked the loss of predicted breeding wetlands under scenarios where either small or hydrologically isolated wetlands were removed from the study area. Six species lost at least half of their breeding wetlands in this landscape if either: 1) all wetlands less than 0.30 ha or 2) wetlands lacking permanent stream connections, were removed from the landscape. Species could lose half of their individual breeding populations and still retain $\geq 94\%$ of their total breeding wetland area if they lost only their smallest-sized breeding wetlands, suggesting that conserving many small-sized breeding wetlands may be more important than retaining fewer, large-sized breeding wetlands for most species. We correlated the relative times of year a species bred and metamorphosed with the median size of their breeding sites to illustrate that early-breeding species use smaller wetlands more often than later-breeding species. Furthermore, early-breeding species had a larger proportion of their breeding sites, and breeding wetland area, among wetlands that lack stream connections than later-breeding species. This study illustrates how legislation that protects only large wetlands, and those with permanent stream connections, can fail to protect amphibian species that breed earlier in the year and contain a large fraction of their breeding populations in small and hydrologically isolated wetlands.

INTRODUCTION

World-wide declines of amphibian populations have been observed for well over a decade, and are proposed to be greater than those observed for both birds and mammals (Stuart et al. 2004). Habitat loss is viewed as the most far-reaching and significant cause of declines (Wake and Morowitz 1991, Blaustein et al. 1994, Dodd 1997, Alford and Richards 1999), although environmental degradation via contaminant exposure (reviewed by Blaustein et al. 2003), the spread of pathogenic disease (Daszak et al. 2003, Lips et al. 2006, Pounds et al. 2006), and the introduction of non-native species (Bradford et al. 1993, Knapp and Matthews 2000, Vrendenburg 2004) have been implicated in declines. Due to the paucity of amphibian species protected under state and federal species listings, the protection of amphibian diversity is largely afforded through legislation that protects wetland habitats (e.g., the Federal Clean Water Act), rather than species-targeted approaches such as the Endangered Species Act. However, amphibian species that breed exclusively in non-flowing waters (i.e., pond-breeding amphibians) are likely to experience habitat loss because the Clean Water Act regulates primarily rivers and streams, and non-flowing waters intimately connected to those water-bodies.

More than half the historic wetlands in the United States have been lost to human development (Tiner 1984, Dahl 1990), and recent trends that report a net gain in total wetland area are misleading because nearly all gains came from the creation of pond-type wetlands on agricultural land (Dahl 2006). The steepest declines in wetlands loss have occurred in freshwater wetlands in the eastern United States, and much of these recent declines have been attributed to the loss of smaller wetlands (< 1 ha) that are exempt from federal protections (Snodgrass et al. 2000). Furthermore, the loss of small wetlands are likely underestimated because the geographic information system (GIS) database used by the U.S. Fish and Wildlife Service to track the status and trends of wetlands in the United States (National Wetlands Inventory database, NWI, <http://www.nwi.fws.gov>) typically does not attempt to map or inventory wetlands smaller than 0.4 ha.

Small wetlands and hydrologically isolated wetlands can be critical components of the landscape for maintaining amphibian biodiversity. Small wetlands frequently offer

unique habitat characteristics such as reduced predator populations (Semlitsch 2000), and their presence on the landscape reduces dispersal distances among breeding ponds thereby increasing gene flow and reducing the probabilities of local extinction of individual wetlands (Dodd and Cade 1998, Leibowitz and Brooks 2008). Hydrologically isolated wetlands (i.e., isolated wetlands) are a special case of wetland habitat that lack permanent stream connections to other surface-water bodies (Winter and LaBaugh 2003), although they can be connected via groundwater or non-channelized surfacewater flow. Over 1/3 of all wetland habitat types are considered isolated wetlands, as well as 13% of all terrestrial system types classified by NatureServe (Comer et al. 2005). Tiner (2003b) found that isolated wetlands accounted for greater than half of all wetlands in 43 of 71 study areas throughout the entire United States, although they typically accounted for less than half of all wetland area. The importance of isolated wetlands as amphibian breeding habitats has been well documented, and they can also function as waterfowl staging and stopover points, maintain metapopulation dynamics for some reptile species, and harbor fauna that are diverse and rarely found in non-isolated wetlands (reviewed by Leibowitz 2003).

Small and isolated wetlands are also ecologically important because they offer a large number of habitat patches for colonization by species. Although metapopulation (Levins 1970, Hanski 1999) and island biogeography theory (MacArthur and Wilson 1967) predicts that larger habitat patches will be inhabited by more species, this relationship is not seen in amphibian assemblages for some study areas (Hecnar and M'Closkey 1996, Lehtinen and Galatowitsch 2000, Snodgrass et al. 2000, Oertli et al. 2002, Weyrauch and Grubb 2004). Furthermore, Oertli et al. (2002) showed that species richness at a landscape level was greater for aquatic plants, gastropods, coleopterans, odonates, and amphibians when preserving numerous smaller-sized ponds than preserving fewer, large ponds of equal cumulative wetland area. However, the preservation of several small wetlands over fewer, large wetlands, may not be a wise conservation strategy if smaller habitats support small populations that are prone to extinction, and are unlikely to be re-colonized.

If small or isolated wetlands harbor unique communities not found in larger wetlands, then protection of these habitats would be necessary to maintain diversity in the landscape. Baber et al. (2004), however, refuted this assertion because they found amphibian assemblages in smaller wetlands included mostly species that were common among larger wetlands. This suggested that assemblages found in small wetlands were the result of sampling a habitat with relatively few species, rather than a habitat with a unique community. Snodgrass et al. (2000), however, failed to find that pattern among isolated wetlands, suggesting that small wetlands contained amphibian species that were uniquely adapted to exploit small wetlands, and these species were much less likely to occur in larger wetlands. If species richness is the only difference between amphibian assemblages in small and large wetlands, then we would expect to see a strong correlation between the number of wetlands a species breeds in, and its total amount of breeding wetland area. If this pattern is not observed, then differences in assemblages between small and large wetlands could be due to species that are able to successfully colonize one wetland type, but not the other.

The proportion of a species' breeding wetlands distributed among small or isolated wetlands can be a function of their availability in the landscape, and the abundance of these wetlands can vary greatly between landscapes. For, example, Calhoun et al. (2003) found the abundance of seasonal pools between study areas in Maine differed by nearly an order of magnitude (13.5 pools/km² compared to 1.4 pools/km²). Thus, it is important to place the loss of breeding wetlands in the context of the overall loss of wetlands in the landscape to draw inferences outside of the study area. Species that use small or isolated wetlands at a rate that is higher than they occur in the landscape will be sensitive to the loss of these wetlands if they are less successful at colonizing other wetlands types. It can be assumed these species meet this assumption because their larvae have been shown to be more susceptible to predators that inhabit large, permanent wetlands (Woodward 1983, Wilbur 1987), and they are competitively inferior to the larvae of other species unless resource availability is low, pond drying regimes are fast, or there is a lack of aquatic predators (Wilbur 1987, Skelly et al. 2002).

In this study, we used spatially-explicit models to evaluate the importance of small and isolated wetlands on the diversity patterns of amphibian assemblages by predicting the occurrence of nine amphibian species in all potential breeding wetlands in NJ-DEWA. These species included the spotted salamander (*Ambystoma maculatum*), red-spotted newt (*Notophthalmus viridescens*), American/Fowler's toad (*Bufo* species), Northern gray treefrog (*Hyla versicolor*), spring peeper (*Pseudacris crucifer*), American bullfrog (*Rana catesbeiana*), green frog (*Rana clamitans*), pickerel frog (*Rana palustris*), and the wood frog (*Rana sylvatica*). We compared the number of wetlands a species was predicted to occupy to the total amount of wetland area they were predicted to occupy to determine if amphibian species found in small wetlands were also commonly found in larger wetlands. To assess the relative sensitivity of different species to the loss of small and isolated wetlands, we tracked losses in predicted breeding wetland abundance and area as: 1) increasingly larger wetlands and 2) hydrologically isolated wetlands were removed from the landscape. We tested whether the amount of breeding habitat lost was related to life history characteristics associated with the time of year each species bred and when their larvae completed metamorphosis. To address whether the pattern we observed might apply to landscapes with different densities of small and isolated wetlands, we compared changes in predicted breeding wetlands to the overall loss of potential amphibian breeding wetlands, and quantified changes in measures of spatial isolation between potential breeding wetlands.

METHODS

Characterization of Potential Amphibian Breeding Sites

Delaware Water Gap National Recreation Area (DEWA) is located in northeastern Pennsylvania and the northwestern New Jersey, and is bisected by the Delaware River. DEWA consists of 28,000 hectares of mostly forested habitat containing hundreds of bodies of water that include a variety of wetland types; natural depressions, beaver ponds, and artificially impounded open water ponds and vegetated wetlands. We created a spatially-referenced database of potential amphibian breeding wetlands that consisted of lentic wetlands identified from aerial photography by DEWA park staff (available at: <http://nrdata.nps.gov/dewa/dewadata/>), or discovered in the field by staff of the Wildlife

Conservation Society, or the USGS Leetown Science Center while conducting surveys of pond-breeding amphibians (Snyder et al. 2004).

From 2001 through 2007, we evaluated all lentic wetlands identified by GIS mapping and field observations for their potential to serve as amphibian breeding habitats. We observed the early spring hydroperiod of each wetland in at least one year, and defined potential breeding wetlands as all lentic wetlands that typically possessed standing water through the month of April (when ambystomatid salamanders lay their eggs). If a potential breeding wetland displayed a fluctuating seasonal hydroperiod, we mapped its flooded perimeter during high-water conditions (typically mid-April) using a handheld, 12-channel, global positioning system (Trimble™ GeoXT unit), and we post-processed resulting pond boundary polygons using differential correction to achieve mean vertex position accuracies of < 1.0 meter RMS error. The size of primarily large (> 1 ha) wetlands with relatively stable hydroperiods were estimated using datalayers of photointerpreted wetlands. The resulting GIS layer of potential amphibian breeding wetlands in NJ-DEWA included 175 potential breeding wetlands with shapes that were derived from GPS mapped pond perimeters ($n = 122$), from GIS datalayers of photointerpreted wetlands ($n = 43$), or represented by point locations of unmapped ponds ($n = 10$).

Hydrologic Regimes, Water Inputs and Wetland Assessments

We assessed the degree of hydrologic connectivity for all wetlands in NJ-DEWA. We defined hydrologic connectivity as the presence of a channelized inflow or outflow of water (a stream channel) into a receiving waterbody. We classified wetlands on a ranked scale as being 1 = strictly isolated, 2 = seasonally connected, or 3 = permanently connected. Strictly isolated wetlands contained no channelized inflow or outflow of surface water. Seasonally connected wetlands possessed a seasonal hydrologic connection that consisted of inflows or outflows that were observed to dry at least once during the year, whereas permanently connected wetlands had at least one channel that had never been observed as dry (even if they potentially could dry during prolonged periods of drought). Observations on the hydrological connectivity of each NJ-DEWA

wetland were made at least once during amphibian surveys conducted between 2001 and 2006, or July of 2007.

We quantified the proportion of the area surrounding each wetland that contained at least 50% forest canopy cover within 25 m (P25), and within 250 m (P250) of their flooded perimeter. This was accomplished by overlaying our amphibian breeding wetland datalayer with a photo-interpreted digital vegetation map of DEWA (Fike 1999; available at: <http://nrdata.nps.gov/dewa/dewadata/>) that delineated and attributed polygons according to their canopy cover class. We chose these metrics of canopy cover because several species of pond-breeding amphibian seem to respond to thresholds of 50% forest canopy cover (Gibbs 1998), and 25 m, and 250 m, buffers approximate proposed seasonal riparian zones and critical upland habitats for vernal pools, respectively (Brown and Jung 2005, Calhoun et al. 2005).

We quantified landscape-level metrics of spatial isolation associated with the total area, abundance, and proximity of wetlands that amphibians could breed in. We quantified the number of potential breeding wetlands within 1 km of the flooded perimeter of each pond or wetland (PONDS1KM). Similarly, we quantified the sum total area of potential breeding wetlands located within 1 km of each wetland's flooded perimeter (AREA1KM), and the nearest edge-to-edge distance to the nearest potential breeding wetland (MINDIST). All spatial isolation metrics were calculated using only a pool of neighbors located in New Jersey because the Delaware River was considered an absolute migration barrier for amphibians. Furthermore, spatial isolation metrics included data on potential breeding wetlands within 1 km outside of the park's boundaries to reduce "edge effects" associated with incomplete spatial data.

Species Occupancy Models

We estimated a probability of occurrence ($\hat{\psi}$) for each of nine species of pond-breeding amphibian at all 175 potential breeding wetlands located in NJ-DEWA. We estimated the probabilities of occurrence by using species occupancy models (MacKenzie et al. 2002) parameterized for each species by Julian et al. (Chapter 1). We created occupancy

models from encounter histories that were constructed from observations of amphibian egg masses, larvae, and breeding adults during surveys of 44 sites in NJ-DEWA from April through July of 2005. For each species, $\hat{\psi}$ was modeled as a best-fit combination of the covariates: wetland size, hydrologic connectivity, forest canopy cover (P25 and P250), and spatial isolation (PONDS1KM) (Table 2.1). Estimates for $\hat{\psi}$ were adjusted by the probability of detecting a species at a site, given that species was present. The estimated probability of detection (p) was a function of combinations of wetland size and fish presence (Table 2.1). To select best-fit models for each species, AIC scores were used to determine the most parsimonious model with a substantial level of empirical support (Burnham and Anderson 2002). Julian et al. (Chapter 1) reported the accuracy for these models typically exceeded the accuracy of models from bird (Klute et al. 2002, Shiner et al. 2002, Hepinstall et al. 2002, Dettmers et al. 2002) and amphibian studies (Kolozyary and Swihart 1999, Suzuki et al. 2008) found in the literature.

Predicting Amphibian Species Abundance and the Implications of the Loss of Small and Isolated Wetlands

If $\hat{\psi}$ for a species exceeded 0.5 at a potential breeding wetland, the species was predicted to occur there, if not, it was considered absent. We did not use the proportion of occupied sites from Julian et al. (Chapter 1) as a cut-off value because they employed a stratified random sampling design, therefore, the proportion of occupied sites surveyed by them would not necessarily be indicative of the proportion of occupied sites throughout NJ-DEWA. We characterized the amount of wetland area (breeding wetland area) for each species by summing the areas of all wetlands in NJ-DEWA where a species was predicted to occur. Likewise, we characterized the abundance of predicted wetlands (number of breeding wetlands) by counting the number of wetlands where a species was predicted to occur. Each species was ordinally ranked according to the time of year they initiated their breeding season (breeding phenology rank), and by the time of year their larvae complete metamorphosis (metamorphosis phenology rank) in NJ-DEWA. The breeding and metamorphosis phenology rankings of each species were then compared to their predicted wetland area and abundance with correlation analysis to

determine if their relative abundance was related to these reproductive life history characteristics.

We estimated the change in wetland abundance and wetland area under scenarios where all wetlands smaller than a given size were removed from NJ-DEWA. Both of these measures were expressed as a proportion of the original amount of wetland that occurred under the scenario of no wetland loss. We estimated the minimum size of protected wetlands necessary to retain 50% of the original wetland abundance, and 50% of the original area for each species. We then correlated these values to the breeding and metamorphosis phenology rankings of species to determine if the effect of losing small wetlands was associated with reproductive life history characteristics. To evaluate how sensitive individual species were to the loss of small wetlands, we compared the trajectories of predicted breeding wetland loss to that of the overall loss in potential breeding wetlands. Additionally, we tracked changes in the spatial isolation of individual wetlands as small wetlands were removed from the landscape. Three measures of spatial isolation (PONDS1KM, AREA1KM, and MINDIST) were tracked by taking the mean value of each of the 175 potential breeding wetlands in NJ-DEWA after removing all other wetlands that did not meet minimum size cut-off values.

We assessed the impact of losing isolated wetlands by characterizing the proportions of predicted wetlands and wetland area found among hydrologic connectivity classes. We correlated the breeding and metamorphosis phenology rankings of each species with 1) the proportion of its breeding wetlands and 2) the proportion of its breeding wetland area that was distributed among strictly isolated wetlands (wetlands completely lacking a stream connection). We also tracked changes in the spatial isolation of individual wetlands (PONDS1KM, AREA1KM, and MINDIST) after strictly isolated wetlands were removed from the landscape.

Comparing Amphibian Communities Between Connectivity Classes

To assess the extent amphibian communities differed between strictly isolated, seasonally connected, and permanently connected wetlands, we calculated Horn's Index of Similarity between these wetland classes using the expected number of wetlands

occupied by each species for each connectivity class. The expected number of occupied wetlands for a species was calculated by summing each species occurrence estimates (i.e., $\hat{\psi}$'s) for all NJ-DEWA wetlands within a connectivity class. Thus, the expected number of occupied sites accounted for the occasional presence of a species at a wetland with a very low probability of occurrence (and vice-versa) because it did not rely on a cutoff value of $\hat{\psi}$ to predict occurrence. This is in contrast to our method for determining the predicted number of occupied sites (see **METHODS: Predicting Amphibian Species Abundance...**), which assigns occupancy status by using a cutoff value of $\hat{\psi}$.

RESULTS

Estimating Wetland Abundance and Impacts of Wetland Loss

A total of 175 potential breeding wetlands were identified in NJ-DEWA, and potential breeding wetlands accounted for a total area of 139.2 ha. Nearly 75% of all wetlands were ≤ 0.5 ha in size, although wetlands of this size accounted for only 17.2 ha, or approximately 13% of all breeding wetland area (Figure 2.1). In contrast, $< 20\%$ of all wetlands were larger than 1.0 ha, although wetlands of this size accounted for $>75\%$ of all potential breeding wetland area. Approximately half of all strictly isolated, and seasonally connected wetlands were smaller than 0.15 ha, and 0.12 ha in size, respectively. Permanently connected wetlands tended to be larger in size, with half of all permanently connected wetlands being 0.37 ha and smaller.

Based on our models, *A. maculatum* was predicted to be able to breed in the greatest number of wetlands and over the largest wetland area (151 wetlands representing 137.9 ha; almost all available breeding wetlands), whereas *Bufo* species was predicted to breed in the fewest wetlands and the smallest area (47 wetlands representing 34.9 ha) (Figure 2.2). Despite the positive trend in relative area and abundance of wetlands for these two species, there was no significant correlation between predicted wetland abundance and area when all species were considered ($r = 0.452$ and $P = 0.222$). This suggested that some common species occurred at more small wetlands than larger ones, whereas some less common species occurred at more large wetlands than smaller ones. A weak,

negative correlation between wetland abundance and breeding phenology rankings ($r = -0.625$ and $P = 0.072$) suggested species that initiated their breeding season earlier in the year occupied more individual wetlands than those who breed later in the season. No other significant correlations existed between breeding or metamorphosis phenology rankings and breeding wetland abundance or area.

For each species, we estimated the minimum size of wetlands that would need to be retained in NJ-DEWA to preserve at least 50% of all breeding wetlands (Table 2.2), and the minimum size to preserve at least 50% of the cumulative area of breeding wetlands (Table 2.3). The median size of predicted *R. sylvatica* breeding wetlands was 0.11 ha. The loss of wetlands smaller than 0.11 ha would reduce the number of *R. sylvatica* breeding wetlands by half, but would only result in a 5% loss of breeding wetland area. In contrast to *R. sylvatica*, all wetlands less than 0.42 ha would have to be lost in this landscape before *R. catesbeiana* would lose half of their breeding sites (Table 2.2). Nearly half of all potential amphibian breeding wetlands in NJ-DEWA are smaller than 0.12 ha, and species most sensitive to the loss of small wetlands included *R. sylvatica*, *P. crucifer*, and *H. versicolor*. The minimum wetland size necessary to preserve half of a species individual breeding wetlands (e.g., the median breeding wetland size) was positively correlated with rankings for both breeding season phenology (early to late) ($r = 0.811$, $P = 0.008$) and metamorphosis phenology (short to long) ($r = 0.854$, $P = 0.003$) (Figure 2.3).

Rana sylvatica required the preservation of the smallest-sized wetlands to retain half of their total breeding wetland area (Table 2.3). If wetlands smaller than 2.4 ha were eliminated or made unsuitable in NJ-DEWA, *R. sylvatica* would lose >50% of their breeding wetland area, and retain 5% of their original number of breeding sites. At the other end of the spectrum, wetlands up to twice the size (e.g., ≥ 4.71 ha) could be eliminated before experiencing a 50% decrease in the predicted breeding wetland area for *P. crucifer*, *N. viridescens*, and *R. catesbeiana*. Wetlands < 4.3 ha in size constituted approximately half of all potential breeding wetland area, but if wetlands of this size were lost then *R. sylvatica*, *H. versicolor*, and *Bufo* species would lose more than half of their

breeding wetland area. The minimum size necessary to preserve half of a species breeding wetland area was not significantly correlated with either breeding season phenology ($r = 0.548$, $P = 0.126$) or metamorphosis phenology ($r = 0.442$, $P = 0.234$).

Sixty-four potential breeding wetlands were classified as strictly isolated, and these wetlands comprised a total of 24.2 ha. Strictly isolated wetlands were more abundant in number than wetlands with seasonal connections or those with permanent connections (Figure 2.4), but only comprised 17.4% of all potential breeding wetland area (Figure 2.5). In contrast, wetlands with permanent connections comprised nearly two-thirds (65.5%) of all wetland area.

If strictly isolated and seasonally connected wetlands were lost from the landscape, six species would lose more than half of their breeding wetlands, and seven would lose at least 25% of their breeding wetland area. Among all species, the proportion of predicted breeding wetlands classified as strictly isolated wetlands was negatively correlated with both breeding phenology rankings ($r = -0.834$, $P = 0.005$), and metamorphosis phenology rankings ($r = -0.738$, $P = 0.023$). Five of nine species were predicted to have $\geq 25\%$ of their breeding wetlands in strictly isolated wetlands (Figure 2.4), but *R. sylvatica* was the only species that was predicted to occupy these wetlands at a rate that exceeded their availability. Wetlands lacking a permanent stream connection were the only wetlands predicted to contain *R. sylvatica* ($\hat{\psi} > 50\%$), and 55% of predicted *R. sylvatica* breeding wetlands were classified as strictly isolated.

The proportion of breeding wetland area classified as strictly isolated was negatively correlated with breeding phenology rankings ($r = -0.738$, $P = 0.023$) and metamorphosis phenology rankings ($r = -0.762$, $P = 0.017$). At least 23% of predicted breeding wetland area for *Bufo* species, *H. versicolor*, and *R. sylvatica* were located in strictly isolated wetlands, whereas *A. maculatum* was the species with the next greatest proportion of its wetland area in this class (Figure 2.5).

If all strictly isolated wetlands in NJ-DEWA were removed, the loss of potential amphibian breeding wetland area would be equivalent to removing all wetlands that are less than 1.08 ha in size, whereas the loss of potential breeding wetland abundance would be equivalent to the loss of all wetlands less than 0.08 ha in size (Figure 2.6). The species that appears to be the most dependent upon strictly isolated wetlands is *R. sylvatica*. If all strictly isolated wetlands were removed from NJ-DEWA, the loss of breeding wetland area for *R. sylvatica* would be equivalent to the loss of all wetlands smaller than 2.7 ha, whereas the loss of breeding wetland abundance for *R. sylvatica* would be equivalent to removing all wetlands smaller than 0.13 ha. In contrast, removing strictly isolated wetlands from NJ-DEWA would not decrease *R. catesbeiana* breeding wetland abundance or area because this species is not predicted to occur in these wetlands (e.g., $\hat{\psi} < 50\%$). Therefore, the effect on *R. catesbeiana* of removing all strictly isolated wetlands is equivalent to removing all wetlands < 0.005 ha.

Community Similarity Between Connectivity Classes

Seasonally connected wetlands contain amphibian communities that are intermediate to those found in strictly isolated and permanently connected wetlands. Values for similarity indices between seasonally connected wetlands and permanently connected wetlands (Horn's Index of Similarity, $R_0 = 0.965$) were similar to indices calculated between seasonally connected and strictly isolated wetlands ($R_0 = 0.949$), whereas communities at strictly isolated wetlands and permanently connected wetlands were the least similar to each other ($R_0 = 0.861$). Among both strictly isolated wetlands and seasonally connected wetlands, the expected number of occupied wetlands was highest for the two earliest breeding species, *R. sylvatica* and *A. maculatum* (Figure 2.7). *Notophthalmus viridescens*, *P. crucifer*, and *H. versicolor* were considerably more common than *Bufo* species, *R. palustris*, *R. clamitans*, and *R. catesbeiana* among strictly isolated wetlands, whereas these seven species were similarly prevalent among seasonally connected wetlands. For wetlands with permanent connections, later breeding species were more common than earlier breeding species, and there was less variability in the expected number of occupied wetlands among species (CV = 25.3%) than observed in seasonally connected (CV = 39.5%) or strictly isolated wetlands (CV = 81.1%).

Wetland Loss and the Spatial Isolation of Breeding Wetlands

The mean breeding wetland area within 1 km of each wetland in NJ-DEWA was 4.74 ha (SD = 64.8), and the mean number of wetlands within 1 km was 6.9 (SD = 4.7) (Figure 2.8). Strictly isolated wetlands had more breeding wetland area within 1 km (mean = 5.20 ha), and more breeding wetlands within 1 km (mean = 8.1 wetlands), than both wetlands with seasonal connections (mean = 3.84 ha and 6.7 wetlands), and those with permanent connections (mean = 5.05 ha and 5.7 wetlands). These trends were surprising given the mean size of wetlands with permanent connections was four times larger than strictly isolated wetlands, and thus, had larger 1-km buffers surrounding them.

Eliminating all wetlands as large 4.1 ha would result in the loss of 50% of wetland area within 1km, whereas eliminating wetlands ≤ 0.12 ha is all that is necessary to reduce the number of wetlands within 1 km by 50% (Figure 2.8). If strictly isolated wetlands were absent, the mean wetland area within 1 km would be reduced by 24.5% to 3.58 ha/km, whereas the mean number of wetlands would be reduced by 42.9% to 3.94 wetlands/km. Without strictly isolated wetlands in the landscape, only one breeding site would be located within 1 km of 10 neighboring wetlands, compared to 39 sites that currently meet that criterion.

The mean minimum distance to a breeding wetland was 184.8m (SD = 192.9). Strictly isolated wetlands had a mean minimum distance (mean = 207.3 m) that was larger than both wetlands with permanent connections (mean = 171.9 m) and seasonal connections (mean = 171.8 m). The mean minimum distance to a wetland would double if wetlands smaller than 0.12 ha were eliminated, triple if wetlands smaller than 0.30 ha were eliminated, and quadruple if wetlands smaller than 0.48 ha were eliminated (Figure 2.9). Correlation analysis showed that wetland size was not related to nearest neighbor distance ($r = -0.043$, $P = 0.569$) or number of wetlands within 1 km ($r = -0.071$, $P = 0.350$), but it was positively related to wetland area within 1km ($r = 0.345$, $P < 0.001$).

If strictly isolated wetlands were removed from the landscape, the mean minimum distance to a breeding wetland would increase by 61.5% to 298.4 m. Also under this

scenario, the mean number of wetlands would be reduced by 42.9% to 3.94 wetlands per km (SD = 2.72), and no individual wetland would exceed 10 wetlands within 1 km. This compares to 22% (39 ponds) of wetlands that would have > 10 wetlands within 1 km under the scenario of no wetland loss. Decreasing the number of wetlands/km to this level is equivalent to losing all wetlands smaller than 0.09 ha (regardless of their hydrologic connectivity). Under the scenario in which strictly isolated wetlands were removed, the mean wetland area would be reduced by 24.5% to 3.58 ha/km (SD = 4.57), and would never exceed 26.7 ha for any one wetland. This compares to 1.7% of individual wetlands (3 ponds) that would have >26.7 ha within 1 km under the scenario of no wetland loss. Decreasing the area of wetlands/km to this level is equivalent to losing all wetlands <1.28 ha.

DISCUSSION

During the last decade, the destruction of wetlands < 0.5 ha accounted for approximately half of the total wetland area lost in the United States (Dahl 2006). This suggests small wetlands are being lost in the landscape at a much faster rate than larger wetlands. It is vital to maintain the presence of small and isolated wetlands at the landscape level because they can represent the majority of breeding wetlands for a majority of pond-breeding amphibian species. Two-thirds of species would lose at least half of their breeding wetlands if NJ-DEWA lost either 1) wetlands smaller than 0.3 ha, or 2) wetlands that lacked a permanent stream connection (strictly isolated and seasonally connected wetlands). Early breeding species would lose relatively more breeding wetlands than late breeding species if small and isolated wetlands were lost in the landscape. The number of breeding wetlands of species like *R. sylvatica* and *P. crucifer* would be reduced in half if wetlands less than 0.15 ha were lost, whereas over 80% of *R. sylvatica* breeding wetlands would be lost if only wetlands with permanent stream connections remained. Although it is a late spring-breeding species, maintaining many small and isolated wetlands in the landscape was also important to *H. versicolor* because the number of wetlands within 1 km was positively related to their occurrence. Furthermore, the actual impact of small and isolated wetland loss on *H. versicolor* could

be much greater than we reported because our simulations of wetland loss did not recalculate POND\$1KM after each removal of a wetland.

The loss of isolated wetlands would result in the loss of distinct amphibian assemblages that are dominated by early-breeding species. Early breeding species may benefit from breeding in wetlands that lack large-bodied, late breeding anurans (notably *R. clamitans* and *R. catesbeiana*) that can prey on their newly metamorphosed juveniles, and have been implicated in the extirpation of some amphibian populations. Strictly isolated wetlands and seasonally connected wetlands are both dominated by early-breeding species, yet seasonally connected wetlands also support large-bodied anuran species more commonly found in wetlands containing permanent stream connections. Therefore, state and community-based inventories of isolated and seasonally connected wetlands (reviewed in Calhoun and Reilly 2008) should not assume these wetlands harbor identical amphibian assemblages, and should place higher conservation value on strictly isolated wetlands if their goal is to preserve amphibian assemblages that are absent from non-isolated wetlands already protected by federal laws (e.g., Clean Water Act legislation).

The most effective means of maintaining amphibian diversity appears to be through the conservation of the greatest number of isolated wetlands in the landscape, and 2) relatively large wetlands (> 0.5 ha) with stream connections. Priority should be placed on conserving a high number of small-sized isolated wetlands because this strategy would maintain more individual breeding populations of species like *R. sylvatica*, *H. versicolor*, *N. viridescens* and *Bufo* species that occur in isolated wetlands at rates that are not influenced by wetland size. This strategy could provide similar benefits to *A. maculatum* whose occurrence is positively related to wetland area, but has a high probability of occurring in small ponds that are surrounded by uplands with > 50% canopy closure (Julian et al. Chapter 1). In contrast, *P. crucifer*, *R. clamitans*, and *R. palustris* would benefit from the protection of large wetlands with stream connections because they are more likely to occur in wetlands with stream connections than isolated wetlands, but seasonally connected wetlands would have to exceed 0.5 ha before each species has a high probability of occurring in them.

Either the loss of small wetlands, or the loss of hydrologically isolated wetlands, would drastically isolate remaining amphibian populations in terms of the number of nearest neighbors and the distance to the nearest neighbor. The removal of all wetlands smaller than 0.20 ha would decrease the number of wetlands within 1 km by more than half (61%) and more than double the average distance to the nearest wetland to 419 m. In a review of the literature, Semlitsch and Skelly (2008) reported that mean seasonal migration distances were below 200 m for nine species of pond-breeding amphibians. If an estimate of juvenile dispersal distance is twice the distance of adult seasonal migrations, then removing wetlands smaller than 0.2 ha in NJ-DEWA could prevent many wetlands from being colonized by adjacent populations. Under the scenario that all wetlands <1 ha are removed, landscapes studied by Gibbs (2000) and Semlitsch and Bodie (1998) would maintain an average distance to the nearest wetland of approximately 600 m. This compares to a distance of 900 m in NJ-DEWA if wetlands < 1 ha are removed. Under this scenario in NJ-DEWA, even highly mobile species such as *R. sylvatica*, whose juveniles can disperse an average of 1.15 km (Colburn 2004), could have a low likelihood of colonizing adjacent wetlands. Occurrence was influenced by spatial isolation for only one species we studied, but spatial isolation could influence the occurrence of additional species if NJ-DEWA were to lose small and isolated wetlands. The loss of small and isolated wetlands would make NJ-DEWA a considerably more fragmented landscape than its current state, and Marsh and Trenham (2001) have proposed that spatial isolation has a greater influence on colonization rates of wetlands in highly fragmented landscapes than relatively undisturbed landscapes.

Several species used small and isolated wetlands in a greater proportion than expected in terms of both the number of available wetlands, and the area of available wetlands. We believe the patterns observed in this study are applicable to other management areas in the northeastern United States. The abundance of small and isolated wetlands in NJ-DEWA is similar to other areas in the northeastern United States, and is an order of magnitude lower than study areas that are exceptionally rich in these habitats (see review in Colburn 2004). This study illustrates how federal Clean Water Act legislation cannot protect amphibian biodiversity because it is designed to prevent the loss of wetlands that

are large (typically > 4 ha [Snodgrass et al. 2000]), maintain a significant nexus to a navigable body of water, and are important to interstate commerce. If all wetlands < 4 ha were removed from NJ-DEWA, one-third of all amphibian species modeled would lose at least half of their breeding wetland area, and two-thirds would lose > 90% of their individual breeding wetlands. If a permanent hydrologic connection is necessary to prove a significant nexus, as argued by Justice Scalia in *Rapanos vs. U.S. Army Corps of Engineers* (126 S. Ct. 2208, 2006), the Clean Water Act could fail to protect more than half of the breeding wetlands of two-thirds of the species studied. Consequently, state and local legislation that protects isolated wetlands could be essential to maintaining amphibian biodiversity at the landscape level.

Table 2.1. Summary of regression coefficients ($\beta \pm 1$ SE) for detection probability (p) and probability of occurrence (ψ) from final occupancy models for nine amphibian species in NJ-DEWA (from Julian et al. Chapter 1).

Species	Detection p			Occurrence ψ					
	SIZE ¹	FISH ²	SIZE X FISH ³	SIZE	CONNECT ⁴	SIZE X CONNECT ⁵	P250 ⁶	P25 ⁷	PONDS 1KM ⁸
<i>A. maculatum</i>	-0.30 ±0.24	-0.72 ±0.40		1.88 ±0.92			3.71 ±1.79		
<i>N. viridescens</i>	1.37 ±0.46						7.80 ±3.45	-7.95 ±2.86	
<i>Bufo</i> species	-1.96 ±0.83							-7.87 ±4.12	
<i>H. versicolor</i>		-2.93 ±1.18						-11.09 ±4.99	1.04 ±0.52
<i>P. crucifer</i>	0.95 ±0.37			9.36 ±1.11	11.94 ±1.60	-3.15 ±0.39			
<i>R. catesbeiana</i>		1.52 ±0.69			2.05 ±0.95				
<i>R. clamitans</i>	1.35 ±0.45	3.07 ±1.91	-1.14 ±0.55	1.96 ±0.92	2.34 ±0.78				
<i>R. palustris</i>				10.85 ±0.67	13.80 ±0.94	-3.34 ±0.20	-8.29 ±2.86		
<i>R. sylvatica</i>		-1.63 ±0.61			-2.15 ±0.79				

¹SIZE: wetland area

²FISH: fish present=1, fish not present=0

³SIZE X FISH: interaction term between SIZE and FISH

⁴CONNECT: strictly isolated=1, seasonal connection=2, permanent connection=3

⁵SIZE X CONNECT: interaction term between SIZE and CONNECT

⁶P250: proportion of forested area within 250 m of flooded perimeter with > 50% canopy cover

⁷P25: proportion of forested area within 25 m of flooded perimeter with > 50% canopy cover

⁸PONDS1KM: number of amphibian breeding wetlands within 1 km of flooded perimeter

Table 2.2. Minimum size of remaining wetlands necessary to retain 50% of predicted breeding wetlands for nine species of amphibians and all potential breeding wetlands (Potential wetlands) in NJ-DEWA.

Species	Minimum wetland size (ha)	Number of wetlands remaining	Wetland area remaining (ha)	Proportion of wetland area remaining
<i>R. sylvatica</i>	0.11	59	45.7	0.95
Potential wetlands	0.14	88	134.3	0.96
<i>P. crucifer</i>	0.15	46	109.5	0.98
<i>H. versicolor</i>	0.18	47	61.4	0.96
<i>A. maculatum</i>	0.22	75	131.9	0.96
<i>Bufo</i> species	0.22	24	33.2	0.95
<i>R. palustris</i>	0.29	37	96.3	0.95
<i>N. viridescens</i>	0.29	46	114.3	0.96
<i>R. clamitans</i>	0.39	43	120.1	0.94
<i>R. catesbeiana</i>	0.42	29	87.0	0.96

Table 2.3. Minimum size of remaining wetlands necessary to retain 50% of predicted breeding wetland area for nine species of amphibians and all potential breeding wetlands (Potential wetlands) in NJ-DEWA.

Species	Minimum wetland size (ha)	Wetland area remaining (ha)	Number of wetlands remaining	Proportion of wetlands remaining
<i>R. sylvatica</i>	2.38	25.8	6	0.05
<i>H. versicolor</i>	3.21	40.1	7	0.07
<i>Bufo</i> species	3.48	18.6	4	0.08
Potential wetlands	4.25	71.9	11	0.06
<i>A. maculatum</i>	4.25	71.9	11	0.07
<i>R. palustris</i>	4.49	53.9	8	0.11
<i>R. clamitans</i>	4.49	67.6	10	0.12
<i>P. crucifer</i>	4.71	57.6	8	0.09
<i>N. viridescens</i>	4.71	63.1	9	0.10
<i>R. catesbeiana</i>	4.71	49.4	7	0.12

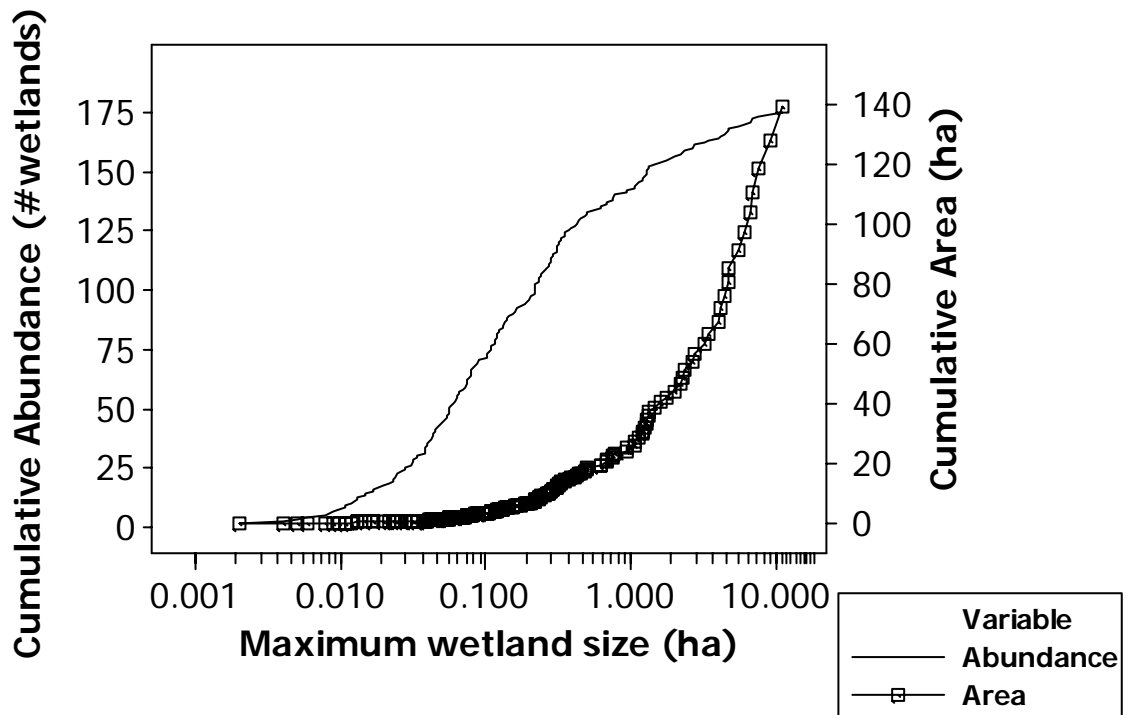


Figure 2.1. Cumulative number of wetlands (Cumulative Abundance) and cumulative wetland area (Cumulative Area) for all potential breeding wetlands of a given maximum wetland size in NJ-DEWA.

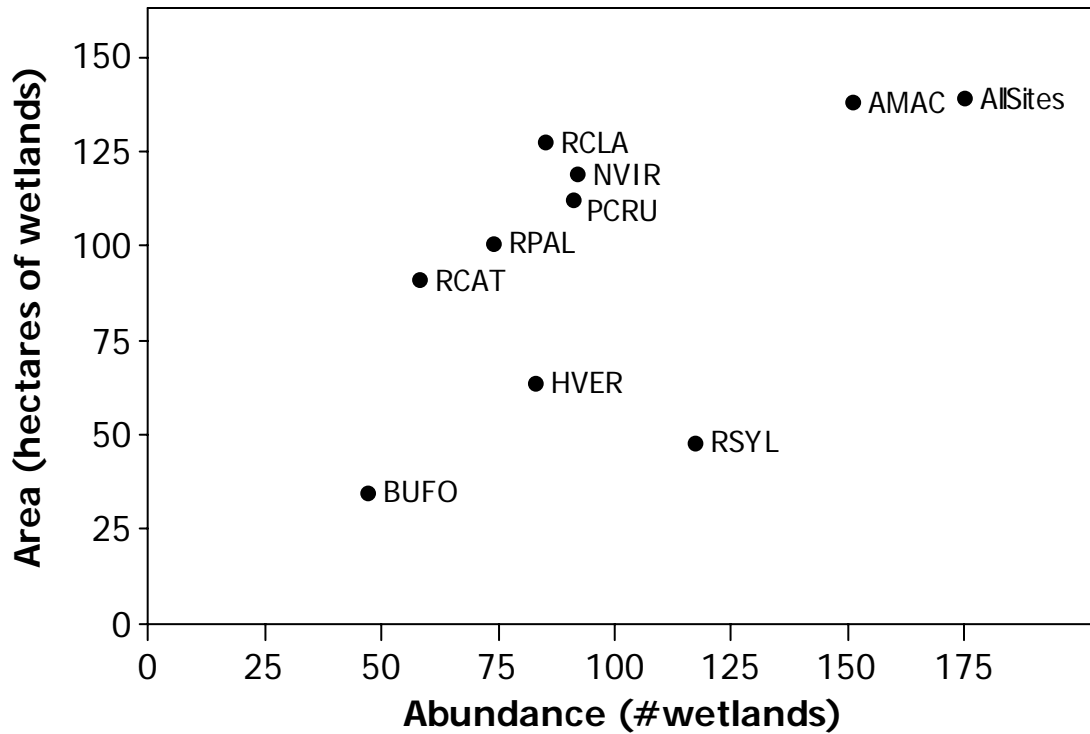


Figure 2.2. The number and total area of predicted breeding wetlands for nine species and all potential breeding wetlands in NJ-DEWA (AMAC *A. maculatum*, BUFO *Bufo* species, HVER *H. versicolor*, NVIR *N. viridescens*, PCRU *P. crucifer*, RCAT *R. catesbeiana*, RCCU *Rana clamitans*, RPAL *R. palustris*, RSYL *Rana sylvatica*, AllSites All potential breeding wetlands).

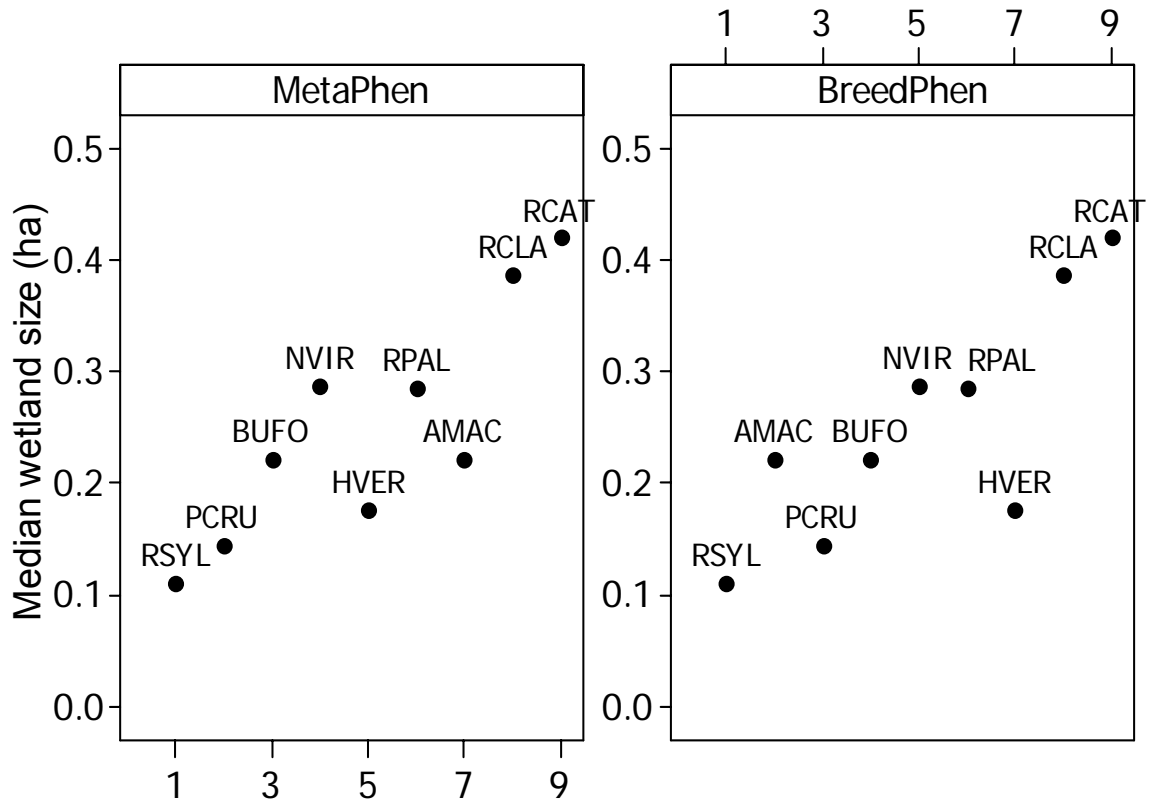


Figure 2.3. Species rankings for metamorphosis phenology (MetaPhen) and breeding phenology (BreedPhen) plotted against the median size of predicted breeding wetlands (in hectares) for amphibian species in NJ-DEWA (AMAC *A. maculatum*, BUFO *Bufo* species, HVER *H. versicolor*, NVIR *N. viridescens*, PCRU *P. crucifer*, RCAT *R. catesbeiana*, RCLA *Rana clamitans*, RPAL *R. palustris*, RSYL *Rana sylvatica*).

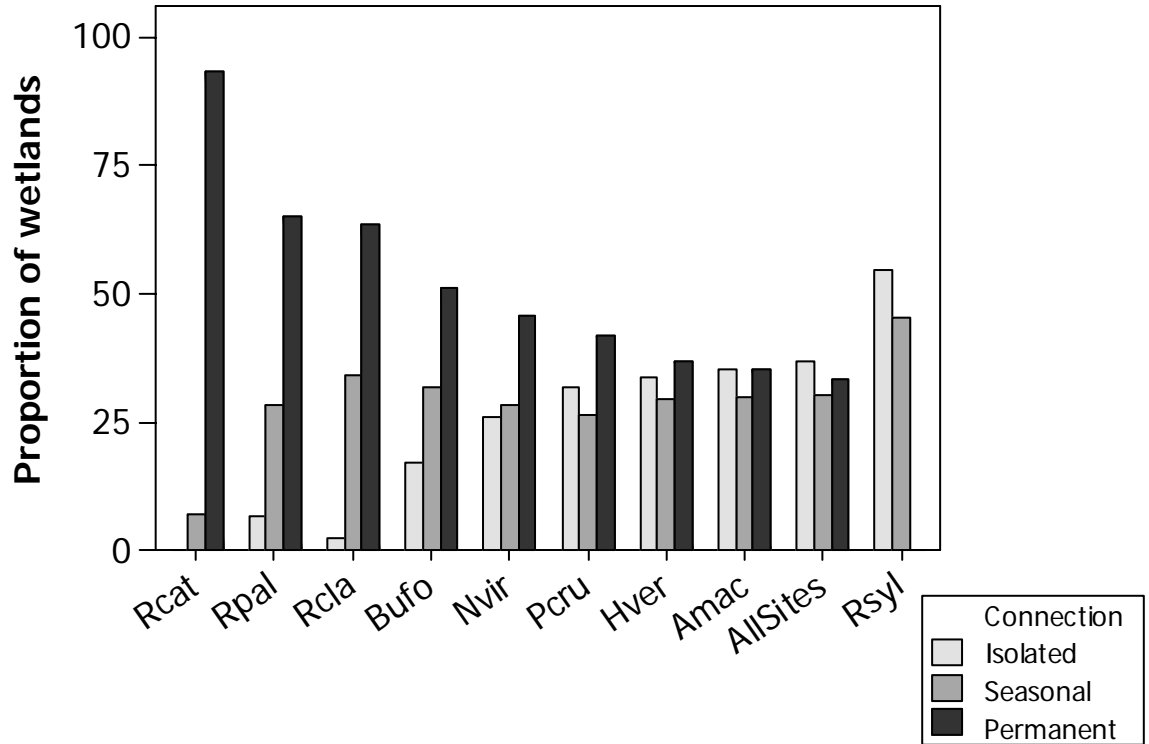


Figure 2.4. The proportion of predicted breeding wetlands distributed among hydrologic connectivity classes in NJ-DEWA (*Amac A. maculatum*, *Bufo Bufo* species, *Hver H. versicolor*, *Nvir N. viridescens*, *Pcru P. crucifer*, *Rcat R. catesbeiana*, *Rcla Rana clamitans*, *Rpal R. palustris*, *Rsyl Rana sylvatica*, *AllSites All potential breeding wetlands*).

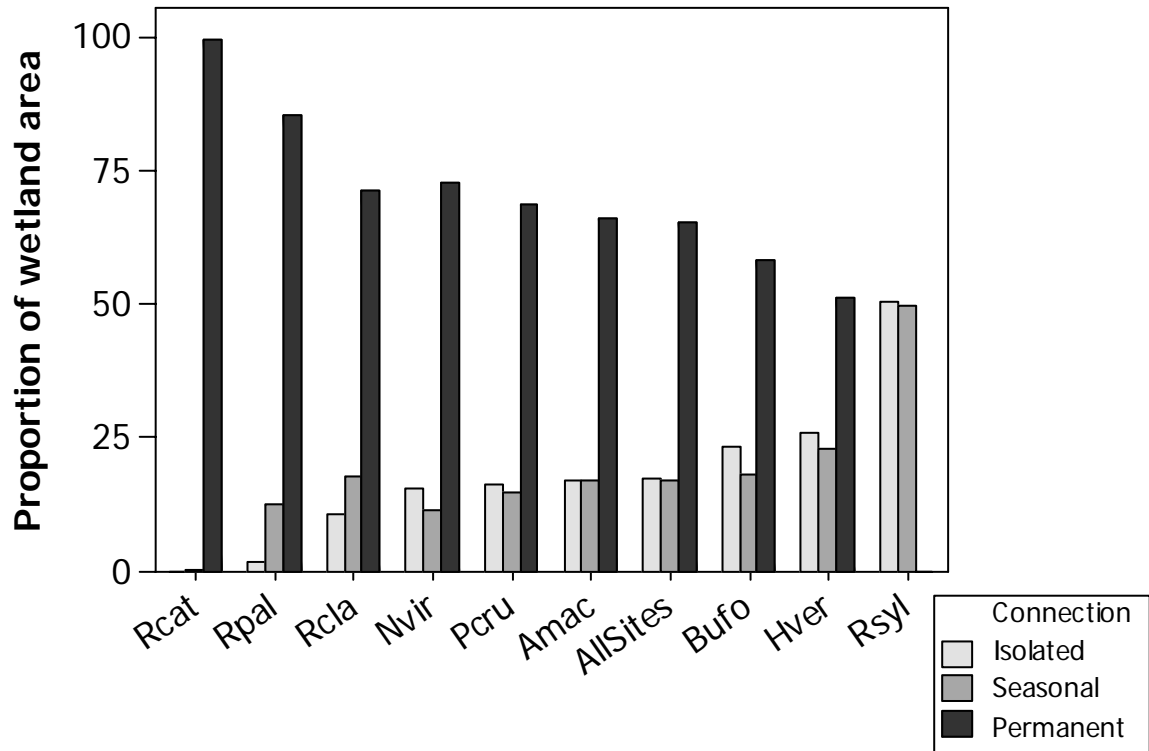


Figure 2.5. The proportion of predicted breeding wetland area distributed among hydrologic connectivity classes in NJ-DEWA (*Amac* *A. maculatum*, *Bufo* *Bufo* species, *Hver* *H. versicolor*, *Nvir* *N. viridescens*, *Pcru* *P. crucifer*, *Rcat* *R. catesbeiana*, *Rcla* *Rana clamitans*, *Rpal* *R. palustris*, *Rsyl* *Rana sylvatica*, *AllSites* *All potential breeding wetlands*).

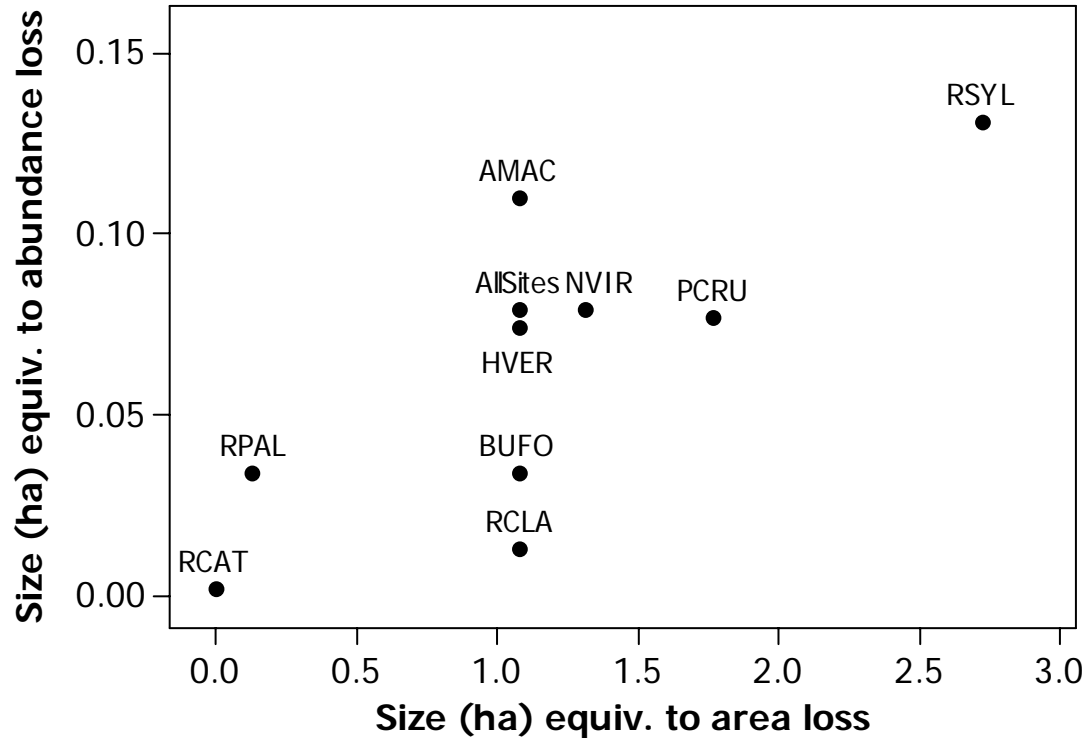
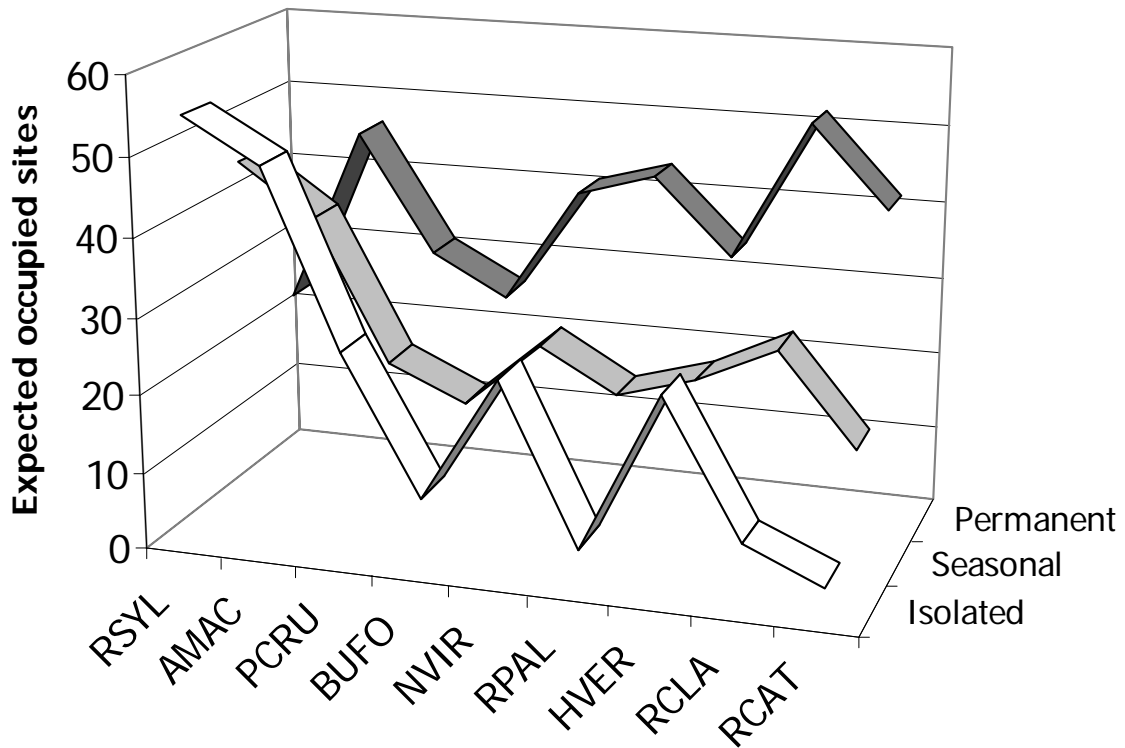


Figure 2.6. Size criteria that would produce equivalent losses in breeding wetland abundance (Y-axis) and wetland area (X-axis) as a loss of strictly isolated wetlands in NJ-DEWA (AMAC *A. maculatum*, BUFO *Bufo* species, HVER *H. versicolor*, NVIR *N. viridescens*, PCRU *P. crucifer*, RCAT *R. catesbeiana*, RCCU *Rana clamitans*, RPAL *R. palustris*, RSYL *Rana sylvatica*, AllSites All potential breeding wetlands).



Breeding phenology (early to late)

Figure 2.7. Expected number of occupied sites by hydrologic connectivity class for 9 species of amphibians among all wetlands in NJ-DEWA (AMAC *A. maculatum*, BUFO *Bufo* species, HVER *H. versicolor*, NVIR *N. viridescens*, PCRU *P. crucifer*, RCAT *R. catesbeiana*, RCCU *Rana clamitans*, RPAL *R. palustris*, RSYL *Rana sylvatica*).

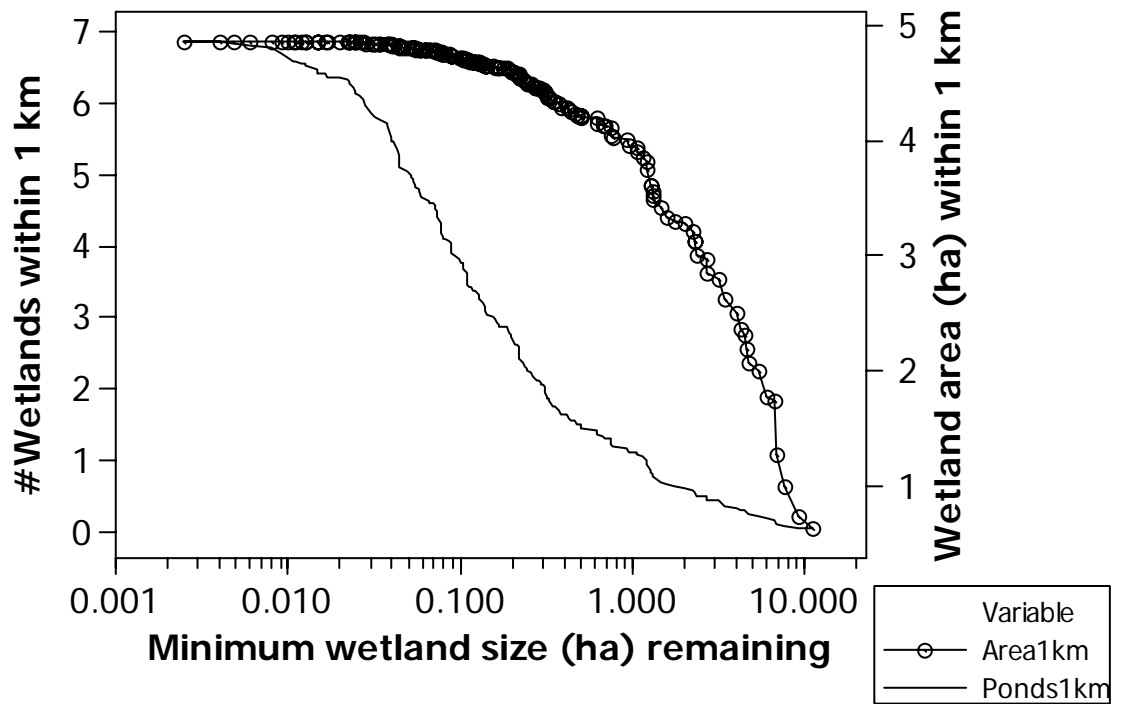


Figure 2.8. Change in 1) the number of wetlands within 1km (Ponds1km) and 2) the wetland area within 1km (Area1km) as a function of the loss of all wetlands of a given size in NJ-DEWA.

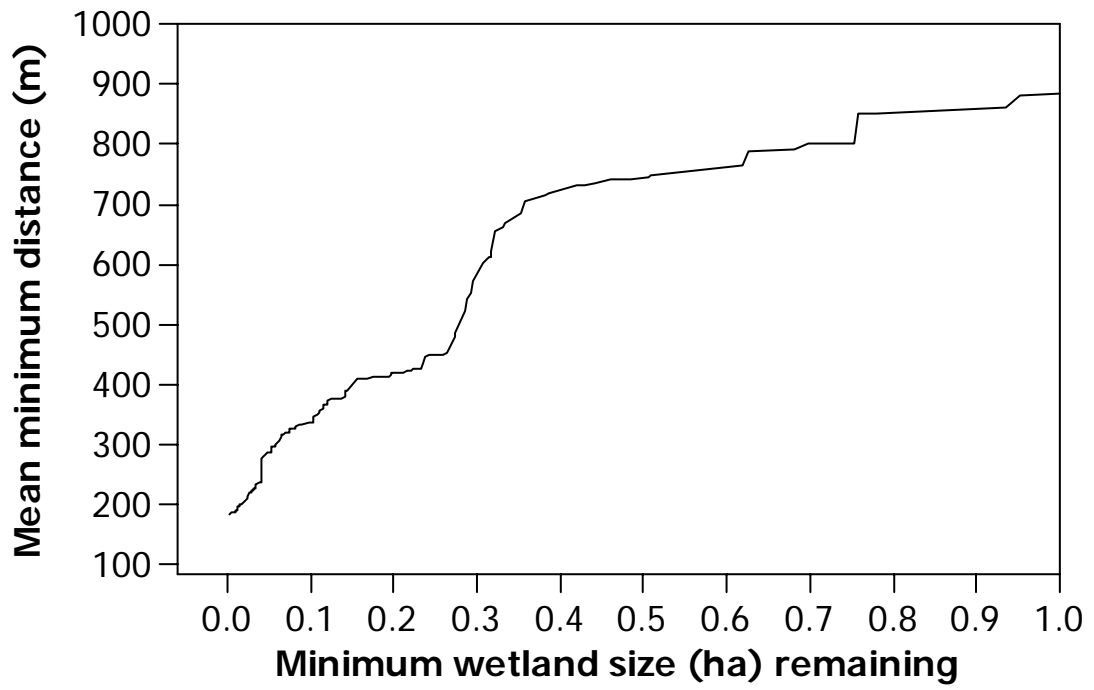


Figure 2.9. Change in the mean distance to the nearest wetland in NJ-DEWA as a function of the loss of all wetlands of a given size.

CHAPTER 3:

Distinguishing the size, hydroperiod, and water chemistry of
isolated and non-isolated wetlands among potential amphibian
breeding wetlands

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ABSTRACT

Recent national trends estimate that half of all wetland area lost is due to the degradation and destruction of small (< 0.5 ha) wetlands. To assess the relative risk of isolated wetlands and non-isolated wetlands to this pattern of wetland loss, we identified, mapped, and characterized the hydrology of 175 lentic (non-flowing) wetlands that could serve as amphibian breeding habitats in the New Jersey portion of the Delaware Water Gap National Recreation Area (NJ-DEWA). We found that 75% of all wetlands were < 0.5 ha in area, yet wetlands of this size only constituted 15% of all wetland area in NJ-DEWA. If this landscape were to follow national trends in wetlands loss, approximately 21 wetlands smaller than 0.5 ha would be degraded or destroyed for every wetland larger than 0.5 ha. This trend would have a significantly greater impact on wetlands that lack permanent stream connections to adjacent waterbodies (i.e., isolated wetlands) because they include relatively more small-sized wetlands than wetlands that contain permanent stream connections. Among isolated wetland types, we found that wetlands with seasonal stream connections were more hydrologically stable and contained surface water with higher pH and conductivity than wetlands that completely lacked stream connections. These results suggest that distinctions should be made between isolated wetlands with seasonal stream connections and those which lack stream connections when assessing the ecological functions and conservation value of individual isolated wetlands because hydroperiod and water chemistry can have a significant influence on amphibian species that occur at wetlands.

INTRODUCTION

Isolated wetlands are wetlands that lack permanent stream connections to adjacent waterbodies (Winter and LaBaugh 2003). They can be more abundant than non-isolated wetlands in total number and area in some landscapes (Tiner 2003a), and contain diverse plant and animal communities that can be highly endemic (reviewed by Leibowitz 2003). Differences between isolated wetlands and non-isolated wetlands in their size, abundance on the landscape, biotic communities, hydroperiods, and water chemistry have warranted conservation strategies that attempt to preserve both isolated and non-isolated wetlands on the landscape. Isolated wetlands that completely lack stream connections are placed in a different category than wetlands with seasonal connections in some wetland classification systems (e.g., hydrogeomorphic model of classification, Brinson 1993), but these systems are not always used by investigators, notably the U.S. Fish and Wildlife Service that is charged with assessing national trends in wetland area. If ecological differences exist between isolated wetland types, then investigators should use wetland classification systems that explicitly make this distinction when assessing their status and trends, ecological functions, and vulnerability to development and degradation because different strategies may be necessary to conserve these habitats.

Investigators studying the most conspicuous vertebrate species in isolated wetlands, amphibians, rarely describe the ecological differences between isolated wetlands that completely lack stream connections, and isolated wetlands that contain seasonal stream connections. This distinction can be important in shaping amphibian communities because Julian et al. (Chapter 1) found the occurrence for four of nine species of pond-breeding amphibians differed between these two isolated wetland types, even after accounting for the influence of upland forest canopy cover, wetland size, and spatial isolation from neighboring wetlands. Furthermore, they found the relationship between species occurrence and wetland size fundamentally differed among these two isolated wetland types for two amphibian species (Julian et al. Chapter 1), and amphibian communities among wetlands with seasonal connections were intermediate to those found in strictly isolated wetlands and those with permanent stream connections (Julian et al. Chapter 2).

In response to Supreme Court interpretations of the Clean Water Act that have diminished the federal protection of isolated wetlands (e.g., *SWANCC vs U.S. Army Corps of Engineers* [531 U.S. 159, 2001]; *Rapanos vs. U.S. Army Corps of Engineers* [126 S. Ct. 2208, 2006]), several states have adopted legislation that affords protection specifically to these wetlands (Christie and Hausmann 2003, Mahaney and Klemens 2008). Community-based, non-legislative approaches to protect isolated wetlands also have increased in popularity (Calhoun and Reilly 2008). These efforts focus on building working relationships between wetland scientists, stewardship organizations, municipal planners, developers, and local citizens to identify isolated wetlands and avoid, minimize, and mitigate the impacts of development on them. The degradation and destruction of isolated wetlands, however, likely will continue. Conservation efforts will need to focus on the identification and protection of isolated wetlands that serve critical habitat functions for biological communities by providing breeding habitats, staging areas for seasonal migrations, and dispersal “stepping stones” to reduce the genetic isolation of breeding populations (Colburn 2004).

Predicting the duration that standing water is present in a wetland, its hydroperiod, is an important component in identifying isolated wetlands that function as breeding habitats for biota. Isolated wetlands must contain standing water for two consecutive months in order to receive protection under state “vernal pool” legislation in New Jersey and Massachusetts. Hydroperiod is the most important factor in determining the biota that colonize and successfully reproduce in a seasonal wetland (Semlitsch et al. 1996, Schneider 1999, Paton and Crouch 2002), and isolated wetlands with long hydroperiods can have more amphibian species than isolated wetlands with shorter hydroperiods (Burne and Griffin 2005a). Investigators have attempted to predict pond hydroperiod for isolated wetlands using basin morphology (Snodgrass et al. 2000, Bilton et al. 2001, Brooks and Hayashi 2002, Skidds and Golet 2005), riparian vegetation (Skelly et al. 2002, Skidds and Golet 2005), and surface water chemistry (Skidds and Golet 2005). These studies group wetlands that lack stream connections with those that contain seasonal connections. Predictions of hydroperiod may be imprecise when using this

inclusive definition of an “isolated wetland” because it includes several hydrogeomorphic (HGM) wetland subtypes (Brinson 1993) that differ in their landscape position, relative contributions of groundwater and surface water to their water budgets, and degree of connectivity to adjacent waterbodies. Most notably, this definition would group isolated depression wetlands that lack stream connections with riparian depression wetlands that contain seasonal stream connections.

It can be difficult to estimate the loss of isolated wetlands in the U.S. based on national trends reported by the U.S. Fish and Wildlife Service (Dahl 1990, 2000, 2006) because freshwater wetlands are categorized by their dominant vegetation type (Cowardin et al. 1979), and gains and losses within these categories of wetlands are expressed in terms of wetland area. As such, national trends from the years 1998 to 2004 that report a net gain in total wetland area are misleading because nearly all gains in area came from the creation of pond-type wetlands on agricultural land (Dahl 2006). It is unlikely that newly created ponds served the same ecological functions as vegetated wetlands because nearly all ponds were designed for freshwater fishing, aesthetic enhancements of developments, retention and detention of surface water, and aquaculture production (Dahl 2006), and less than 2% of created ponds ever develop into vegetated wetland types (Dahl 2000), primarily because of excessive water depths. The loss of wetlands smaller than 0.4 ha (1 ac) in size accounts for 52% of all freshwater wetland area lost from 1998 to 2004, and it can be assumed this trend has a disproportionate effect on isolated wetlands because the majority of isolated wetlands in many study areas are <0.25 ha in size (Colburn 2004). Furthermore, the number of wetlands of this size are often underestimated in inventories, and thus the actual loss is likely underestimated. If, however, isolated wetlands are to be managed as complexes of several nearby wetlands (as recommended by Gibbs and Reed 2008), then quantifying the loss of the total number of isolated wetlands in a landscape may be more important than quantifying the loss of total area.

In this study, we describe how wetlands that: 1) lack stream connections, 2) contain seasonal stream connections, and 3) contain permanent stream connections in the New Jersey portion of the Delaware Water Gap National Recreation Area (NJ-DEWA) differ

in size, abundance, hydroperiod, and water chemistry. We compared the ratios of small to large-sized wetlands along this hydrologic connectivity gradient to quantify the relative likelihood these wetland types will be lost in the landscape under the assumption that small-sized wetlands are the most likely to be degraded or developed. If wetlands that lack stream connections are more likely to be lost in the landscape than wetlands with seasonal stream connections, then higher priority should be placed on them within the framework of programs that protect isolated wetlands. If wetlands from each class of stream connection differ in their hydroperiod and water chemistry across size gradients, then resource managers and development planners will need to establish different morphometric criteria between isolated wetlands that lack connections and those with seasonal connections when assessing their ecological function.

METHODS

Characterization of Potential Amphibian Breeding Wetlands

Delaware Water Gap National Recreation Area (DEWA) is located along the banks of the Delaware River, and is located in both northeastern Pennsylvania, and the northwestern New Jersey. This federally protected area is approximately 28,000 hectares in size, it is heavily forested, and it contains over 300 wetlands and bodies of water that can be used by amphibians for breeding. We used a spatially-referenced database of potential amphibian breeding ponds in DEWA (Julian et al. Chapter 2) to characterize the amount of potential breeding wetland area (i.e., wetland area) and the number of potential breeding wetlands (i.e., wetland abundance) in five wetland size classes: < 0.1 ha, 0.1 – 0.5 ha, >0.5 – 1 ha, >1 – 2 ha, and > 2 ha. Size classes were chosen based on ecological literature that suggest: seasonal wetlands > 0.1 ha contain ecologically long hydroperiods (Brooks and Hayashi 2002), wetlands 0.5 ha and 1.0 ha in area approximate the lower and upper limits of the minimal mapping unit for 1:58,000 scale aerial photographs used to map forested wetlands available in the National Wetlands Inventory database (NWI, <http://www.nwi.fws.gov>), and wetlands 2.0 ha in area approximate the minimal mapping unit for 1:80,000 aerial photography used in the NWI database for this area.

Hydrologic Connectivity, Stability, and Water Chemistry Parameters

We assessed the degree of hydrologic connectivity for each wetland in the New Jersey portion of DEWA (NJ-DEWA). We classified wetlands on a ranked scale as being 1 = strictly isolated, 2 = seasonally connected, or 3 = permanently connected, as described in Julian et al. (Chapter 2). Strictly isolated wetlands contained no channelized inflow or outflow of surface water. Seasonally connected wetlands possessed a seasonal hydrologic connection that consisted of inflows or outflows that were observed to dry at least once during the year, whereas permanently connected wetlands had at least one channel that had never been observed as dry (even if they potentially could dry during prolonged periods of drought).

From June 16 through June 24 in 2005, we assessed the hydrologic stability of 125 potential breeding wetlands located in NJ-DEWA. Hydrologic stability was assessed on a ranked scale that visually estimated the observed area of a wetland relative to its maximum area observed during high-water periods (mid-April). June hydrologic stability for a wetland was scored as either $\leq 10\%$, 11-50%, 51-90%, or $> 90\%$ of its maximum area. We chose to assess hydrologic stability during the month of June because at least two native species of frog in NJ-DEWA can metamorphose by then (*Pseudacris crucifer* and *Rana sylvatica*), and hydrologic assessments at later times in the year can produce very little variation among seasonal wetlands (the vast majority were dry).

We measured surface water conductivity and pH at a total of 111 wetlands during two separate amphibian studies conducted in NJ-DEWA (Snyder et al. 2004, Julian et al. Chapter 1). We took all measurements during high-water periods in 2001, 2002, 2003, and 2005, although not all wetlands were sampled during the same year. We measured conductance with a YSI model 33 temperature/salinity/conductivity meter (YSI Inc., Yellow Springs, Ohio, USA) and the data was converted to specific conductivity ($\text{ms}\cdot\text{sec}^{-1}$ at 20°C) for comparison. We measured the pH of each site with an Orion model 230A pH meters equipped with Orion model 9107BN pH probes (Thermo Fisher Scientific Inc., Waltham, Massachusetts, USA). In instances when water chemistry

parameters were recorded in more than one year for a wetland, maximum values for these parameters were used in data analysis.

Data Analysis

To assess the relative threat of the development of small wetlands to each connectivity class, we used contingency chi-square analysis to detect significant differences ($\alpha = 0.05$) in their proportion of wetlands among size classes. If no difference was detected, then we assumed that isolated and non-isolated wetlands are equally at-risk. If a difference was detected using observations from all three connectivity classes, we omitted observations from one connectivity class to determine if the two remaining connectivity classes were similar in their size class ratios (Zarr 1996).

To describe the relative difference in hydrologic stability between wetlands that differ in connectivity and size, we used ordinal logistic regression analysis to predict hydrologic stability. We entered June stability ranks (JUNESTABILITY) into our models as an ordinal response variable (1 = $\leq 10\%$, 2 = 11-50%, 3 = 51-90%, 4 > 90% of maximum area), and we entered hydrologic connectivity (CONNECT) as a ranked predictor variable (1 = isolated wetland, 2 = seasonal connection, 3 = permanent connection) in addition to hectares of wetland area (LOGAREA) that were obtained from the amphibian breeding wetland GIS datalayer and log transformed. Predicted event probabilities for each observation were converted to cumulative event probabilities that estimated the probability that a wetland would display a given JUNESTABILITY ranking or higher, and odds ratio estimates were used to relate cumulative event probabilities to wetlands of different sizes and connectivity classes (e.g., an isolated wetland was X times more likely to retain $\geq 50\%$ of its area than a seasonally connected wetland) (Hosmer and Lemeshow 2000, McCullagh 1980). Our model did not meet the proportional odds assumption of ordinal logistic regression analysis ($\chi^2 = 6.68$, $df = 4$, $P = 0.15$).

We used multiple linear regression to determine how much variation in surface water pH and specific conductivity was explained by hydrologic connectivity (CONNECT) and wetland size (LOGAREA). Initial regression models included interaction terms between

CONNECT and LOGAREA that were not significant predictors of either pH ($P = 0.270$) or specific conductivity ($P > 0.302$), therefore, final models only included terms for CONNECT and LOGAREA.

RESULTS

In NJ-DEWA, small wetlands were more abundant than larger-sized ones, but accounted for relatively little total wetland area (Figure 3.1). The number of wetlands within each connectivity class were similar, but permanently connected wetlands were three times larger in mean and median size than either isolated or seasonally connected wetlands (Table 3.1). Wetlands with permanent connections differed in their proportion of wetlands among size classes ($\chi^2 = 34.103$, $DF = 8$, $P < 0.001$) from other connectivity classes (Figure 3.2), and had a ratio of small (< 0.5 ha) to large (> 0.5 ha) wetlands (1.2:1) that was lower than that of isolated wetlands (6.9:1) and seasonal wetlands (4.3:1). Strictly isolated wetlands and seasonally connected wetlands were similar in their distributions among size classes ($\chi^2 = 5.483$, $DF = 4$, $P = 0.241$), and there were more wetlands among small size classes than in large size classes (Figure 3.2). There were 1.26 wetlands/km² in NJ-DEWA when considering wetland from all connectivity classes, whereas the density of wetlands that lacked a permanent hydrologic connection was 0.84 wetlands/km².

Logistic regression models indicated that larger wetlands retained more of their original surface area (had higher JUNESTABILITY scores) than smaller ones, and those with more permanent hydrologic connections retained more surface area than more isolated ones ($G = 54.2$, $df = 2$, $P < 0.001$) (Table 3.2, Figure 3.3). Among isolated wetlands surveyed in June of 2005, we observed that 63% had dried completely, compared to 52% of seasonally connected wetlands that were dry, and only 1 of 31 wetlands with permanent connections (Figure 3.4). Wetland size and JUNESTABILITY was correlated in wetlands with seasonal connections (Pearson correlation: $r = 0.455$, $P = 0.002$), but not correlated among strictly isolated wetlands ($r = 0.232$, $P = 0.099$), or wetlands with permanent connections ($r = 0.134$, $P = 0.471$). Despite these differences, a logistic regression model that included an interaction term between CONNECT and LOGAREA was not significant (P

= 0.235), therefore, we cannot infer an interaction between wetland size and connectivity when predicting JUNEStABILITY.

Wetland size and connectivity explained little of the variation in surface water conductivity ($R^2 = 8.4\%$), and slightly more of the variation in surface water pH ($R^2 = 13.3\%$). Wetland size and connectivity were predictors of specific conductivity (Table 3.3), with conductivity decreasing with wetland size, but increasing with connectivity (Figure 3.5) even though these two predictors were positively correlated with each other ($r = 0.352$, $P < 0.001$). Connectivity, alone, was a predictor of pH (Table 3.3), and more hydrologically isolated wetlands had lower pH values than those with more permanent connections (Figure 3.5).

We found the relationship between hydrologic stability and water chemistry parameters differed among hydrologic connectivity classes. Specific conductivity was correlated with June stability scores among wetlands with seasonal connections ($r = 0.610$, $P < 0.001$), but wasn't correlated among isolated wetlands ($r = 0.160$, $P = 0.310$) nor wetlands with permanent connections ($r = 0.170$, $P = 0.428$). In a similar manner, pH was correlated with June stability scores among wetlands with seasonal connections ($r = 0.427$, $P = 0.015$), and was not correlated among isolated wetlands ($r = 0.282$, $P = 0.074$), nor wetlands with permanent connections ($r = 0.255$, $P = 0.288$). However, both specific conductivity and pH were significantly correlated with June stability scores when analyses included either isolated wetlands with seasonally connected wetlands (specific conductivity, $r = 0.351$, $P = 0.002$; pH, $r = 0.337$, $P = 0.004$), or seasonally connected wetlands with wetlands that had permanent connections (specific conductivity, $r = 0.340$, $P = 0.010$; pH, $r = 0.397$, $P = 0.002$).

DISCUSSION

Small (< 0.5ha) amphibian breeding wetlands are likely to be degraded and destroyed at much greater rates (up to 21 times) than larger breeding wetlands in landscapes similar to NJ-DEWA. This is because small wetlands were three times more abundant than larger wetlands while accounting for only 15% of the total wetland area, and the loss of

wetlands < 0.5 ha accounts for half of all wetland area lost nationally (Dahl 2006). Small-sized breeding wetlands are important in maintaining amphibian diversity in NJ-DEWA because they represent the majority of breeding wetlands for all species, and the loss of these wetlands would quadruple dispersal distances to the nearest wetland (Julian et al Chapter 2). National trends in small wetlands loss will have a greater effect on early-breeding amphibian species than species that breed later in the year because the former tend to use small wetlands more often (Julian et al. Chapter 2). This could result in a severe range reduction of these species that were once common across the landscape. The higher rate of wetland loss among small wetlands than larger ones means that isolated wetlands will be at greater risk to degradation and destruction than non-isolated wetlands because of their smaller size. This disparity indicates that legislative measures meant to specifically protect isolated wetlands are necessary to curb the accelerated loss of these important habitats. However, we found that, among isolated wetlands, the risk of wetlands loss was equivalent for wetlands that lack stream connections (strictly isolated wetlands) and those that contained seasonal connections, because of they contain a similar distribution of ponds of different size classes.

The loss of amphibian breeding habitats could be worse in landscapes in the northeastern United States that have more isolated wetlands (i.e., vernal pools) than NJ-DEWA. The density of wetlands without permanent hydrologic connections in NJ-DEWA (0.84 wetlands/km²) was less than densities of vernal pools in landscapes studied by Brooks et al. (1998) (1.1 pools/km²) in northcentral Massachusetts, Calhoun et al. (2003) (1.4 pools/km²) in central Maine, Stone (1992) and Portnoy (1987) (1.9 and 5.8 pools/km² respectively) and Calhoun et al. (2003) (13.5 pools/km²) in southern Maine. More than 80% of vernal pools inventoried by both Brooks et al. (1998) and Calhoun et al. (2003) were smaller than 0.1 ha.

Stream connections and wetland size were important predictors of hydrologic stability, and differences between strictly isolated and seasonally connected wetlands should be considered when assessing the ecological functions of isolated wetland. Strictly isolated wetlands were 5 times less likely to retain as much of their surface area as similarly sized

wetlands with seasonal stream connections, and 25 times less likely to retain as much area as wetlands with permanent connections. This pattern is likely explained by differences in the relative contribution of groundwater to their water budgets. Wetlands with strong groundwater inputs tend to have longer hydroperiods than wetlands with relatively greater surface water contributions, and strictly isolated wetlands tend to have relatively less groundwater contributions than wetlands with stream connections to adjacent water bodies (Biggs et al. 1994, Cole et al. 1997, Gay 1998, Cole and Brooks 2000). This trend is likely the case among amphibian breeding wetlands in NJ-DEWA because connectivity was positively related to surface water conductivity, and high surface water conductivity can be indicative of wetlands with strong ground water contributions (Bay 1967, Gay 1996).

Within the same connectivity class, small wetlands were approximately half as likely to be as hydrologically stable (i.e. retain as much surface area) as wetlands that were an order of magnitude larger in size. There was a significant relationship between surface area and hydrologic stability among isolated wetlands studied by Brooks and Hayashi (2002) ($r = 0.564$), Stidds and Golet (2005) ($r = 0.34$), and Bilton et al. (2001). However, depression wetlands studied by Snodgrass et al. (2000) did not exhibit this relationship ($r = 0.05$). We found a correlation between size and hydrologic stability among seasonally connected wetlands, but not with other connectivity classes. It is likely that wetlands with permanent connections in NJ-DEWA show very little variation in drying scores because a large number of these are human-impounded ponds created to retain water year-round. In contrast, the hydroperiods of strictly isolated wetlands varied greatly, similar to observations by Brooks and Hayashi (2002) among isolated wetlands < 0.1 ha in size.

Predicting wetland hydroperiod can be difficult, and attaining the desired hydroperiod has been identified as the most difficult aspect of vernal pool (i.e., isolated wetland) creation (Beaulieu 2006). Riparian vegetation can strongly influence water loss due to evapotranspiration; surficial geology and soil texture of basins in perched wetlands can influence water loss via infiltration; the influence of groundwater inputs can be highly

variable between HGM wetland subtypes; and investigators have yet to adequately assess the influence of catchment basin size on hydroperiod in isolated wetlands (Brooks 2005). Brooks and Hayashi (2002) identified pond morphologies indicative of isolated pools with hydroperiods long enough to establish faunal communities, but admitted the application of their criteria could be geographically limited. Instead of predicting an individual pond's hydroperiod, our study should be used to compare the relative hydrologic stability of wetlands that differ in size and degrees of hydrologic connectivity. This could be important in wetland remediation programs that intend to create wetlands with hydroperiods similar to destroyed/degraded wetlands that have different dominant water sources (groundwater vs. surface water) or landscape positions (different HGM class or subclass).

Wetland size and hydrologic connectivity were related to surface water conductivity and pH. Therefore, evaluating the ecological function of wetlands should consider hydrologic connectivity because water chemistry parameters have been associated with amphibian species occurrence (Clark 1985, Rowe and Dunson 1993, Horne and Dunson 1994). Both pH and conductivity increased with a wetland's degree of hydrologic connectivity, and these relationships were consistent with predictions that strictly isolated wetlands had the lowest groundwater contributions, and wetlands with permanent connections had the greatest. Surface water pH (Bay 1967, Gay 1996) and conductivity (Palik et al. 2001, Amon et al. 2002, O'Driscoll and Parizek 2003) are greater in groundwater-fed wetland systems than in surface water-fed systems. Within each connectivity class, conductivity increased as wetland size decreased (Figure 3.5), and we attribute this trend to relatively greater groundwater contributions in small wetlands than larger ones. Brooks (2005), working in isolated wetlands, hypothesized that small wetlands will have greater groundwater contributions than larger wetlands due to higher perimeter to surface area ratios. Under high-water conditions, smaller wetlands offer relatively more area for surface water – groundwater exchange than larger wetlands because exchanges tend to occur at flooded perimeters (Millar 1971). In addition, if catchment basins are larger for large wetlands than smaller ones (as Brooks 2005 suspected among isolated wetlands), then large wetlands would have lower conductivities

because they receive relatively greater amounts of surface water runoff than smaller wetlands.

Correlations between June stability scores and water chemistry parameters suggest that conductivity and pH would be most useful in predicting hydroperiod among wetlands with seasonal hydrologic connections, but much less effective for other wetlands. Skidds and Golet (2005) proposed that conductivity could be used, in part, to predict hydroperiods in seasonal wetlands because hydroperiod was positively correlated with conductivity ($r = 0.27$), yet pH was not. We suspect the correlation between conductivity and hydroperiod they observed was influenced mostly by the inclusion of seasonally connected wetlands with strictly isolated wetlands because our inclusion of seasonally connected wetlands with either strictly isolated wetlands or wetlands with permanent connections, resulted in similar correlations.

Isolated wetlands lacking stream connections and those containing seasonal connections offer unique contributions to maintaining amphibian diversity across the landscape of NJ-DEWA because their amphibian communities differ (Julian et al. Chapter 2). This difference in amphibian communities can be attributed more to differences in hydroperiod and water chemistry parameters associated with hydrologic connectivity than wetland size because these two isolated wetland types were similar in their ratios of small to large-sized wetlands. Therefore, the distinction between these two isolated wetland types is essential when resource managers and development planners assess the ecological value and functions of isolated wetlands. However, our research does not suggest that national trends in small wetlands loss translates to a higher likelihood of losing one of these isolated wetland types over the other. Therefore, defining isolated wetlands broadly as wetlands that lack permanent connections appears sufficient in a legislative context, and in the context of community-based efforts to conserve these habitats, but efforts to inventory and map isolated wetlands should make the distinction between strictly isolated and seasonally connected wetlands to better assess the ecological functions, hydrologic conditions, and biotic communities individual wetlands provide.

The federal government's current methods for tracking national wetlands loss fails to account for associated losses in ecosystem functions despite the mandate of the Clean Water Act to "restore and maintain the chemical, physical, and biological integrity of the Nation's waters". This failure is partially attributed to the use of a wetland classification system (Cowardin et al. 1979) that does a poor job of linking functionality to wetland types (Dahl 2006). Although the linkage of wetland functions to wetland type is stronger for classification systems that explicitly use the presence of stream connections in their categorization (e.g., HGM), the loss of ecosystem functions due to wetland loss has been assessed for large watersheds (Tiner 2005) by enhancing the NWI database with individual wetland descriptors for landscape position, landform, water flow path, and waterbody types (LLWW descriptors). Adding LLWW descriptors to wetland databases that use the Cowardin classification system would be an important step in identifying isolated wetlands and assessing their ecological functions in a landscape.

In this process, investigators enhance NWI databases by merging them with U.S. Geological Survey GIS datalayers, and then following dichotomous keys for LLWW descriptor assignment. This process can become labor-intensive if investigators have to interpret aerial photography in order to assign descriptors, but the ecological information added to wetland datalayers could markedly improve predictions concerning the biota and hydrology of individual wetlands.

Table 3.1. Summary statistics for wetland size, specific conductivity, and pH among wetlands sampled in NJ-DEWA from different hydrologic connectivity classes.

Variable	Connectivity	N	Mean	Median	Min	Max	SD	Total
Wetland size (ha)	Isolated	64	0.379	0.085	0.004	7.019	1.194	24.245
	Seasonal	53	0.450	0.120	0.002	4.254	0.832	23.835
	Permanent	58	1.572	0.369	0.005	11.267	2.433	91.150
Specific conductivity ($\text{ms}\cdot\text{sec}^{-1}$)	Isolated	47	99.1	60.0	20.0	423.3	98.1	NA
	Seasonal	34	118.4	72.1	28.4	436.8	104.1	NA
	Permanent	30	164.5	115.5	20.0	584.3	140.7	NA
pH	Isolated	46	6.03	5.92	4.20	8.82	0.17	NA
	Seasonal	34	6.38	6.63	4.42	8.56	0.18	NA
	Permanent	30	7.04	7.13	4.48	10.22	0.23	NA

Table 3.2. Logistic regression coefficients from modeling June stability ranks (JUNESTABILITY) as a function of hydrologic connectivity (CONNECT) and wetland area (LOGAREA) in NJ-DEWA.

Predictor variable	$\beta \pm SE$	Wald χ^2	df	P-value
CONNECT	-1.62 \pm 0.28	34.58	1	< 0.001
LOGAREA	-0.58 \pm 0.28	4.18	1	0.041

Table 3.3. Regression coefficients for linear regression models that predict water chemistry parameters as functions of wetland area and hydrologic connectivity for wetland sampled in NJ-DEWA.

Parameter	Predictor	$\beta \pm$ Std. error	t-statistic	P-value
Specific conductivity	Constant	155.97 \pm 53.70	2.90	0.004
	Connectivity	42.09 \pm 13.91	3.03	0.003
	LogArea	-34.55 \pm 17.65	-1.96	0.053
pH	Constant	6.239 \pm 0.561	11.13	>0.001
	Connectivity	0.577 \pm 0.143	4.04	>0.001
	LogArea	-0.277 \pm 0.183	-1.52	0.133

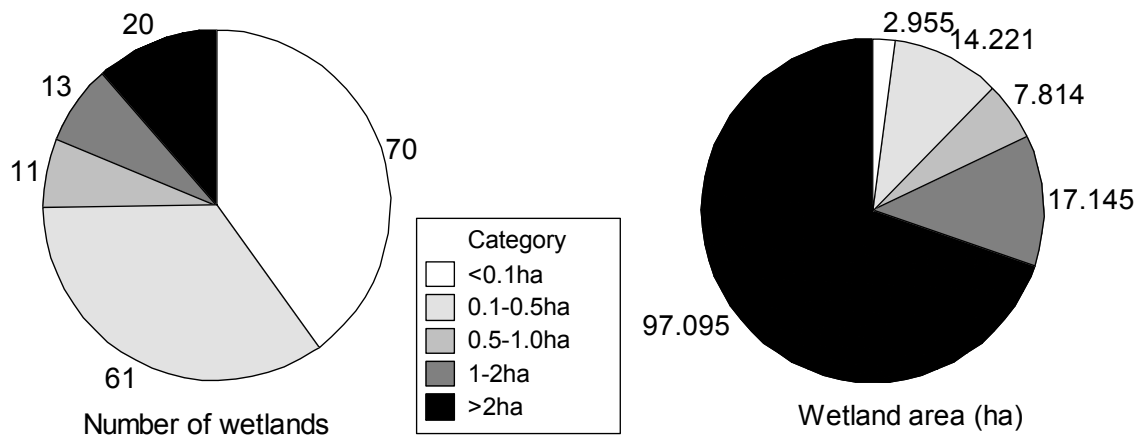


Figure 3.1. Total number of wetlands and amount of wetland area (ha) within size classes for all wetlands in NJ-DEWA.

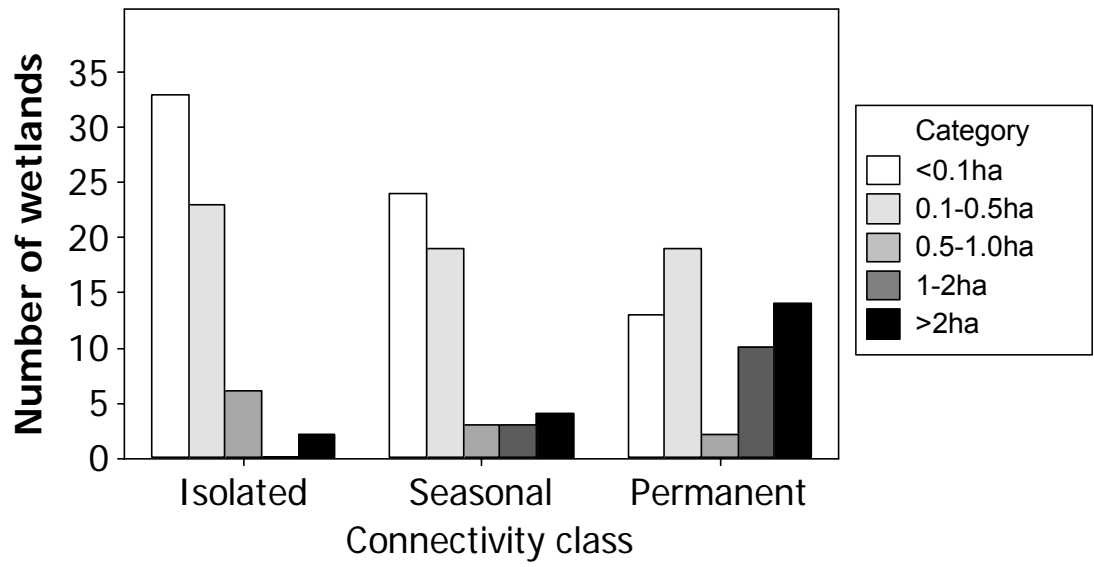


Figure 3.2. The distribution of strictly isolated wetlands (Isolated), seasonally connected wetlands (Seasonal), and wetlands with permanent stream connections (Permanent) among wetland size classes for all wetlands in NJ-DEWA.

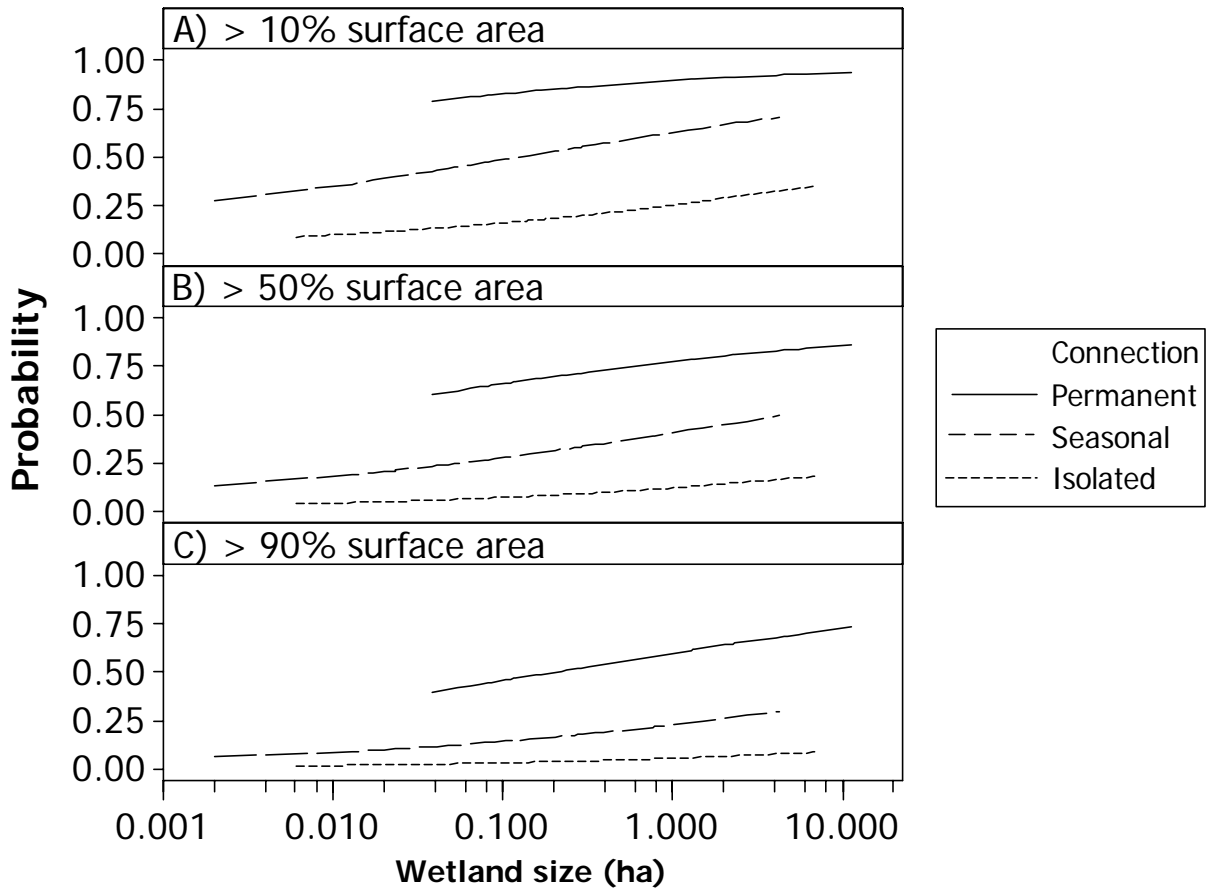


Figure 3.3. Logistic regression model predictions for the probability a wetland will retain at least A) 10%, B) 50%, or C) 90% of its estimated maximum surface area in mid-June as a function of wetland size for wetlands with permanent stream connections (Permanent), seasonal connections (Seasonal), and strictly isolated wetlands (Isolated) sampled in NJ-DEWA in June of 2005.

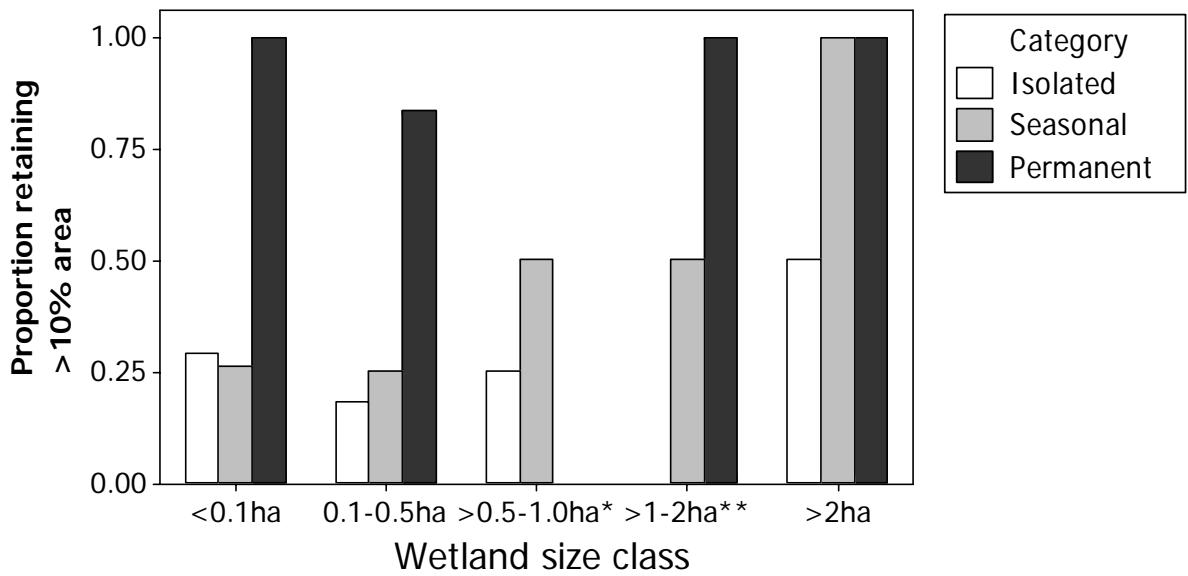


Figure 3.4. Observed proportion of wetlands in NJ-DEWA that retained at least 10% of their estimated maximum surface area in mid-June of 2005 by wetland size and hydrologic connectivity class.

* no drying scores recorded for wetlands with permanent stream connections in this size class

** no strictly isolated wetlands in NJ-DEWA were in this size class

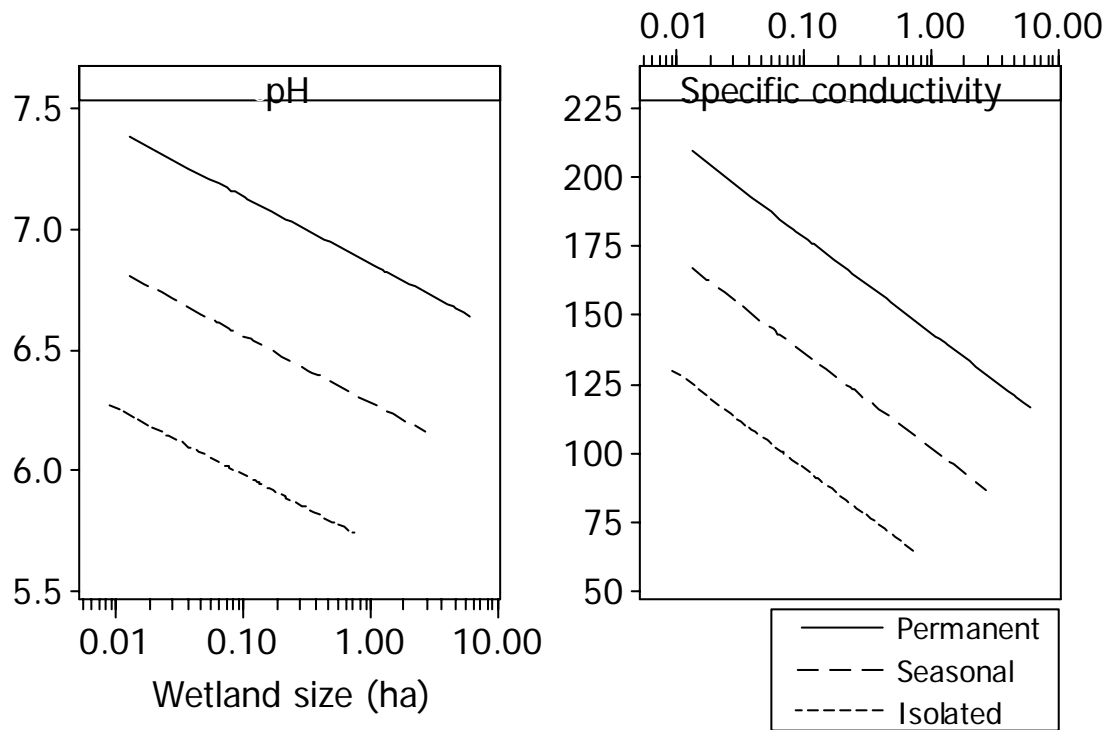


Figure 3.5. Predicted pH and specific conductivity ($\text{ms}\cdot\text{sec}^{-1}$ at 20°C) values as a function of wetland size for wetlands with permanent stream connections (Permanent), seasonal connections (Seasonal), and strictly isolated wetlands and in NJ-DEWA.

CHAPTER 4:

Using wetlands classification and wetland size to identify
amphibian breeding ponds on geographic information system
wetland maps

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ABSTRACT

Geographic information system databases (i.e., datalayers) that are available to the public are a likely means of identifying amphibian breeding ponds for investigators who lack the resources or expertise to interpret aerial photography themselves. However, investigators should be aware of the likelihood small ponds will be omitted from these datalayers, and efficient means of determining which wetland polygons could serve as breeding ponds. We field-verified 336 amphibian breeding ponds in the Delaware Water Gap National Recreation Area (USA), and used logistic regression to estimate the probability a breeding pond would be included on a datalayer as a function of its size. A datalayer based on interpretations of 1:12,000 aerial photography failed to detect 36% of ponds smaller than 0.1 ha, but was able to detect ponds an order of magnitude smaller than the National Wetlands Inventory Database (NWI, based on 1:58,000 aerial photography) with the same level of accuracy. Investigators could use our empirical models to estimate the number of amphibian breeding ponds not included on datalayers, and our models suggest that national trends in wetland loss (based on National Wetlands Inventory) may underestimate by two-fold the relative rate of small wetlands loss (wetlands < 0.5 ha) to large wetlands loss. Secondly, we used classification tree analysis (CART) to identify breeding ponds among wetland polygons using datalayer attributes of wetland size, and Cowardin Class and Water Regime Modifier. CART sorted NWI wetland polygons first by water regime, then class, and then wetland size, to produce trees that misclassified only 25.3% of polygons, and indicated that likely breeding ponds are at least temporarily flooded, classified as either forested or open water wetlands, and at least 0.1 ha in size. CART sorted wetland polygons from 1:12,000 imagery by hydroperiod first, and then wetland size, but produced misclassification rates (23.3%) that were comparable to the use of only Cowardin Class to identify breeding ponds (23.9%). We also evaluated the ability of an airborne light detecting and ranging (LiDAR) sensor to delineate breeding ponds not included on aerial photography datalayers. We found that predictions of flooded areas by LiDAR data were as accurate for ponds detected on datalayers, as they were for ponds that were not detected (at both scales). Thus, LiDAR appears to have the potential to increase the number of breeding ponds detected by 1:12,000 and 1:58,000 scale aerial photography.

INTRODUCTION

Small, seasonal ponds are important breeding habitats for several species of amphibians, and techniques have been developed to identify these habitats across the landscape through the photo interpretation of aerial photography (Stone 1992). These techniques allow investigators to describe the abundance and distribution of amphibian breeding habitats across the landscape (Kent and Mast 2005), quantify changes in habitat abundance over time (Burne and Lathrop 2008), and calculate spatial isolation metrics for these habitat patches (Baldwin et al. 2006). If investigators pursue these objectives and lack the resources or expertise to interpret aerial imagery themselves, they will likely make use of publicly available Geographic Information System (GIS) wetland maps (i.e., datalayers) to identify potential amphibian breeding ponds. Because these datalayers have different criteria of identifying wetlands, it is important for investigators understand: 1) the limits to which these datalayers can detect small ponds, and 2) how to discriminate amphibian breeding ponds from other wetlands that have flooding regimes that are too short to accommodate the aquatic stage of amphibian larvae.

Publicly available wetland datalayers are often based on the interpretation of color infrared (CIR) photography, and their usefulness will depend on the scale of the imagery, the expertise of the photo-interpreter, and the descriptive attributes assigned to individual wetland polygons. The U.S. Fish and Wildlife Service's National Wetlands Inventory database (NWI, <http://www.nwi.fws.gov>) is based largely on 1:58,000 scale CIR photography for the northeastern U.S., and is used to track national trends in wetlands loss (Dahl 1990, 2000, 2006). The minimum mapping unit of this datalayer is 0.4 ha (1 ac) for open water and emergent wetlands in deciduous forest habitats (Tiner 1990), and thus, NWI is most useful in detecting relatively large amphibian breeding ponds.

However, NWI will occasionally identify wetlands < 0.4 ha in size, and knowing the rate small breeding ponds go undetected could help resource managers better estimate the number of these habitats in the landscape. Such estimates would be particularly helpful in developing goals for seasonal "vernal" pool inventory programs that attempt to identify, geo-reference, and field-certify these habitats.

Wetland datalayers interpreted from finer-scale CIR photography are available for some study areas through state or federal agencies (e.g., U.S. National Park Service data available at <http://nrdata.nps.gov/>). However, interpretation of high resolution images can result in the identification of wetlands with flooded conditions that are too short for amphibians to successfully breed in. Thus, eliminating these wetlands out of a pool of potential breeding ponds through field verification can be tedious and costly. In such cases, investigators will need to rely on wetland polygon attributes that describe dominant substrate vegetation and suspected hydroperiod to discriminate potential breeding ponds from other wetlands. The Cowardin wetlands classification system (Cowardin et al. 1979) was developed by the U.S. Fish and Wildlife Service, and many publicly available wetland datalayers use this classification system to attribute wetland polygons. Several authors suggest several Cowardin wetland types (i.e., Classes) that are the most likely to be seasonal breeding ponds (Burne and Lathrop 2008, Calhoun et al. 2003, Calhoun and DeMaynadier 2004). However, we could only identify one study (Calhoun et al. 2003) that quantifies the accuracy of these predictions. Identifying attributes within publicly available wetland datalayers that are indicative of breeding ponds could provide investigators with a better way of balancing the cost of visiting wetlands that are unsuitable breeding ponds, with the benefit of identifying a greater number of breeding ponds in the landscape.

Some airborne sensors that send and sense returns using their own power source (active sensors) have the potential to discriminate flooded areas from non-flooded areas (Townsend 2001, Julian et al. 2009), and these technologies could prove more effective at mapping small amphibian breeding ponds than CIR photography. Notably, Julian et al. (2009) used data from a light detection and ranging (LiDAR) sensor equipped with a green-light laser (Wright and Brock 2002) to discriminate amphibian breeding ponds from adjacent uplands in Delaware Water Gap National Recreation Area, USA. Their approach used only the signal intensity of LiDAR sensor returns and spatial variations in signal intensities to predict areas of standing water (e.g., breeding ponds) mapped by Global Positioning Satellite (GPS) equipment during the time of LiDAR flyovers. Although they quantified the accuracy of breeding pond predictions in the context of

pond size and in-pond vegetation, they did not assess whether accuracy differed between ponds detected by aerial photography, and those that were not. If there is no difference in accuracy between detected and non-detected breeding ponds, and detected ponds are larger than non-detected ponds, this would suggest that LiDAR could be used to improve the mapping of ponds that are too small to be detected by aerial photography.

In this study, we evaluated the use of 1:58,000 and 1:12,000 photo-interpreted GIS wetland datalayers to locate field-verified amphibian breeding ponds in Delaware Water Gap National Recreation Area. For each set of wetland datalayers, we: 1) modeled the relationship between breeding pond size and the probability it would be detected, 2) quantified the amount of unmapped breeding ponds, 3) created decision trees based on wetland size and Cowardin attributes to discriminate breeding ponds from other wetlands, and 4) compared the accuracy of LiDAR-based predictions of flooded areas near ponds detected in datalayers, to predictions of flooded areas near ponds that were not detected in datalayers.

METHODS

Characterization of Amphibian Breeding Ponds

Delaware Water Gap National Recreation Area (DEWA) is a 28,000 ha federally designated recreation area that straddles the Delaware River in northeastern Pennsylvania and northwestern New Jersey. Elevation ranges from 84 – 490 m, and the topography consists mostly of terraced benches, ravines, and ridges, in addition to many floodplains. Forest cover is dominated by upland deciduous forests of oak (*Quercus* spp) and maple (*Acer* spp) mixed with pine (*Pinus* spp), with abundant stands of eastern hemlock (*Tsuga canadensis*). Potential breeding ponds for pond-breeding amphibians (i.e., breeding ponds) were identified from a pool of lentic wetlands within the boundaries of DEWA that were either found on GIS datalayers of photo-interpreted wetland maps, or discovered by field crews while conducting research on pond-breeding amphibians. GIS datalayers of photo-interpreted wetlands included the NWI datalayer based on 1:58,000 CIR photography, and a GIS datalayer compiled by the staff of the Natural Resources

Division of DEWA (NPS-DEWA datalayer, available at: <http://nrdata.nps.gov/dewa/dewadata/>) based on 1:12,000 CIR photography.

From 2001 through 2007, we evaluated all lentic wetlands identified by GIS mapping and field observations for their potential to serve as amphibian breeding ponds. We observed the early spring hydroperiod of each wetland in at least one year, and defined breeding ponds as all lentic wetlands that typically possessed standing water through the month of April (when ambystomatid salamanders lay their eggs). We mapped the flooded perimeters of 217 breeding ponds with seasonally-variable hydroperiods during high-water periods (typically mid-April) using a handheld, 12-channel, global positioning system (Trimble™ GeoXT unit), and we post-processed resulting pond boundary polygons using differential correction to achieve mean vertex position accuracies of < 1.0 m RMS error. The resulting GIS of amphibian breeding ponds in DEWA (PhibHab datalayer) included a total of 336 wetlands whose shapes were either derived from GPS mapped pond perimeters (n = 217), incorporated from NWI or NPS-DEWA datalayers (n = 101), or represented by point locations of unmapped ponds (n = 18).

Because breeding ponds were defined only by the presence of non-flowing water and hydroperiod, they included several hydrogeomorphic (HGM) wetland types (Brinson 1993). Breeding ponds included depression wetlands that are located within closed topographic contours (i.e., topographic depressions). Depression wetlands that lacked channelized inflows or outflows for surface water (i.e., isolated depressions), were largely found in forested ponds and devoid of vegetation, whereas those with at the least seasonal, canalized inflows and outflows (i.e., riparian depressions) were more likely to contain significant in-pond tree, shrub, and emergent vegetation. Breeding ponds also included human and beaver-impounded wetlands. Impounded wetlands in forested ponds typically had concave, mud-bottom basins, and those in more open landscapes contained fringing wetlands dominated by tussocks of emergent vegetation in sections of their shoreline. A relatively small number of breeding ponds were located in floodplains and had direct surface-water connections to headwater streams (i.e., headwater floodplain wetlands). These wetlands were typically associated with prior beaver activity (former

beaver impounded wetlands with breached dams), and were dominated by tussocks of emergent vegetation of sedges and rushes.

Evaluation of NPS-DEWA and NWI Datalayers

We determined the fraction of breeding pond polygons in the PhibHab datalayer that were included on 1) the NWI and 2) the NPS-DEWA datalayer. To determine this, we first overlaid the PhibHab datalayer onto the NWI datalayer in a GIS using ArcView v 3.3 software (<http://www.esri.com>). We then used the “Identity” operation available in X-tools extension for ArcView (<http://www.odf.state.or.us/sfgis>) to label breeding ponds in the PhibHab datalayer that were in contact with a portion of at least one NWI wetland polygon. Likewise, we overlaid the PhibHab datalayer onto the NPS-DEWA datalayer to identify breeding ponds included among NPS-DEWA wetland polygons.

We used logistic regression to model the relationship between the size of a breeding pond and the probability the pond would be included on: 1) the NWI datalayer, and 2) the NPS-DEWA datalayer, separately. These analyses included observations on 276 breeding ponds with either GPS-mapped perimeters (n = 217), or photo-interpreted perimeters (from NWI or NPS-DEWA datalayer) with dimensions that were similar to our field observations (n = 59). The predictor variable in models was the log-transformed GIS-based area estimate for each pond, the binary response variable was whether the pond was “included” (1) or “not included” (0) on the wetlands datalayer in question, and all analyses were performed using MINITAB v. 14.

We used classification tree analysis (CART) to create decision trees that used wetland size and attributes of the Cowardin wetland classification system to identify breeding ponds from the NWI and NPS-DEWA datalayers. To classify wetlands in the NWI datalayer as a breeding pond, we overlaid the NWI datalayer onto the PhibHab datalayer and performed “Identity” operations. Likewise, we performed overlay and “Identity” operations with the NPS-DEWA and PhibHab datalayers to identify breeding ponds on the NPS-DEWA datalayer. Occasionally, multiple wetland polygons on a datalayer were assigned to the same PhibHab breeding pond because all wetland polygons that

intersected a portion of a breeding pond on the PhibHab datalayer were considered to be breeding ponds.

Classification tree analysis is a nonparametric technique that produces a series of recursive, dichotomous splits of observations based on values of predictor variables that increasingly maximize homogeneity in the response variable within a group (Breimen et al. 1984, De'ath and Fabricius 2000). Results are illustrated in classification tree diagrams where a cutoff value of a single predictor variable at the node of a split represents the criteria used to group observations. At a node, a cutoff value for each predictor variable is determined whether that predictor was previously used to group observations or not. The variable that explains the most amount of variation is chosen to split observations at that node, and the vertical length of the branch proceeding the node represents the relative amount of variation explained by that split of the data.

In our CART models, observations were wetland polygons from respective GIS datalayers, the binary response variable was whether a polygon was categorized as a breeding pond (1) or not (0), and the predictor variables were GIS area estimates of wetlands, their Cowardin Class, and Water Regime Modifier. Cowardin Class is used to classify the dominant in-pond vegetation of wetlands, whereas Water Regime Modifier is used to classify the suspected hydroperiods. In CART models, we used Class Modifier as a categorical variable that included Forested (FO), Scrub/schrub (SS), Emergent (EM), and Open Water (OW) classifications. We transformed Water Regime Modifier to a ranked scale of progressively longer hydroperiods by which; 1 = saturated, 2 = intermittently flooded, 3 = temporarily flooded, 4 = seasonally flooded/saturated, 5 = seasonally flooded, 6 = semi-permanently flooded, 7 = intermittently exposed, 8 = permanently flooded. We generated all classification trees using S-PLUS 2000 software.

LiDAR Model Predictions

Julian et al. (2009) used data collected from an airborne LiDAR sensor to derive spatially-explicit models (i.e., LiDAR models) to discriminate flooded areas from upland areas at 24 amphibian breeding ponds (i.e., LiDAR ponds). LiDAR models used logistic

regression to estimate the probability LiDAR return signals came from a flooded area based on a signal's return strength (i.e., intensity), and its degree of spatial autocorrelation with nearby signals. For each LiDAR pond, they quantified the proportion of correctly classified return signals that were located: 1) within the flooded perimeter of ponds (sensitivity score), and 2) within the upland habitat 25 m from the flooded pond perimeter (specificity score). As a third measure of model accuracy, they quantified how frequently return signals located within a flooded perimeter were assigned a higher probability of being flooded than signals located within the surrounding upland habitat (concordance scores). Thus, sensitivity scores related to the proportion of correctly predicted flooded area, specificity scores related to the proportion of correctly predicted upland area, and concordance scores related to the ability to discriminate flooded areas from upland areas.

We classified LiDAR ponds from Julian et al. (2009) as being included or not-included on: 1) the NWI datalayer, and 2) the NPS datalayer. For each datalayer, we compared LiDAR model accuracy (i.e., sensitivity, specificity, and concordance scores from their “*Autocorr*” model) between ponds included and not included on the datalayer, and significant differences for each measure of accuracy were assessed using a Kruskal-Wallis Test (non-parametric one-way analysis of variance). If we failed to detect significant differences ($P > 0.05$) in accuracy between included and non-included LiDAR ponds on a datalayer, then it suggested that LiDAR could be used to increase the number of wetlands detected by aerial photography at that scale.

RESULTS

Characterization of Amphibian Breeding Ponds

We identified 336 amphibian breeding ponds in DEWA. The total area of breeding ponds in DEWA (based on the 276 ponds used in logistic regression analysis) exceeded 196.9 ha. Ponds ranged in size by four orders of magnitude (range = 0.001 - 11.8 ha, median = 0.189, mean = 0.71 ha, $SD \pm 1.59$), and the distribution of these ponds was skewed towards smaller sizes (skewness = 4.2, kurtosis = 20.82). Three-quarters of these ponds were ≤ 0.5 ha in size, and one-third were ≤ 0.1 ha (Figure 4.1). Wetlands ≤ 1.0 ha

represented nearly one-quarter of all breeding pond area, and ponds ≤ 0.5 ha, despite their abundance, comprised only 15.9% of the breeding pond area (Figure 4.1). Breeding ponds ≤ 0.5 ha, however, comprised nearly twice as much acreage (31.2 ha) as larger wetlands of 0.5 – 1.0 ha (16.2 ha).

Breeding Pond Size and Occurrence on Wetlands Datalayers

The NWI datalayer included only half of all potential breeding ponds, and failed to include some breeding ponds as large as 1.6 ha. NWI included 88.5% of pond area (174.3 ha), but failed to include a large fraction of breeding ponds < 0.1 ha in size (87.5%), in addition to those between 0.1 – 0.5 ha in size (43.2%) (Table 4.1). Even ponds that were above the NWI's minimum mapping unit threshold of 0.5 ha were missed 14.5% of the time (Table 4.2), and there was only a 74% chance of detecting a pond 0.5 ha in size (Figure 4.2). Wetland size was positively associated with the probability that a breeding pond would be included on the NWI datalayer ($\beta_{\log\text{Area}} = 2.41 \pm 0.32$, $G = 115.3$, $df = 1$, $P < 0.001$), and this probability decreased rapidly for ponds < 1.0 ha in size. Logistic regression analysis predicted a breeding pond 0.2 ha in size would only have a 50% chance of being included on the NWI datalayer, whereas a pond 0.1 ha in size would have only a 32% chance of being included (Figure 4.2).

Wetland polygons on our most comprehensive datalayer, NPS-DEWA, contained 84.8% of all breeding ponds (regardless of size), and included all breeding ponds that exceeded 0.62 ha. The NPS-DEWA datalayer included 98.7% of all breeding pond area (194.2 ha in total) because the vast majority of breeding ponds that were not included on this datalayer (83.3%) were < 0.1 ha in size. Over one-third of breeding ponds ≤ 0.1 ha were not included on the NPS-DEWA datalayer (Table 4.1 and Table 4.2), compared to only 4% of breeding ponds > 0.1 ha (Table 4.2). The NPS-DEWA datalayer was particularly efficient at detecting wetlands between 0.1 ha and 0.5 ha in size, and failed to detect only 5.4% of these ponds (Table 4.1). Wetland size was positively associated with the probability that a breeding pond would be included on the NPS-DEWA datalayer ($\beta_{\log\text{Area}} = 2.57 \pm 0.39$, $G = 63.1$, $df = 1$, $P < 0.001$), and this probability dropped off precipitously for ponds < 0.1 ha in size. Logistic regression analysis predicted that a

breeding pond 0.1 ha in size would have an 86% chance being included on the NPS-DEWA datalayer, whereas a pond 0.02 ha in size would only have a 50% chance of being included (Figure 4.2).

Identifying Breeding Ponds on Wetlands Maps

Nearly half (n = 147) of all wetland polygons on the NWI datalayer (N = 318) were classified as breeding ponds. Cowardin Class was available for 317 NWI polygons, whereas Water Regime Modifier was available for only 88. Approximately two-thirds (68.6%) of OW wetlands (n = 105) were classified as breeding ponds, whereas SS (n = 43) and FO (n = 146) wetlands were 3.3 and 3.7 times less likely, respectively, to be breeding ponds than OW wetlands (Table 4.3). Of all wetland types, EM wetlands (n = 23) were the least likely to be breeding ponds. Among NWI wetlands with Water Regime Modifiers, 46.6% were classified as breeding ponds. The proportion of wetlands classified as breeding ponds generally increased between modifiers with longer hydroperiods, although seasonally flooded wetlands were less likely to be breeding ponds than either temporarily flooded or seasonally saturated/flooded wetlands (Table 4.4). More than half of all wetlands with at least temporarily flooded hydroperiods were breeding ponds (Table 4.5).

In CART, Water Regime Modifier was used to initially split NWI wetlands into breeding and non-breeding pond categories used, whereas secondary and tertiary splits used Class and wetland size, respectively (Figure 4.3). Thirty-six of 41 breeding ponds in this analysis were FO and OW wetlands ≥ 0.091 ha in size, with hydroperiods that were temporarily flooded or longer. A classification tree containing seven groupings of wetlands (i.e., terminal nodes) misclassified only 25.3% of wetlands, identified 92.7% of wetland polygons that were not breeding ponds, and identified 78.9% of polygons that were breeding ponds. In comparison, when Class, alone, was used to categorize breeding ponds it produced a misclassification rate of 34.1% because OW wetlands were the only Class predicted to be breeding ponds (Table 4.4). Furthermore, categorizing breeding ponds by Class was less accurate than CART at identifying polygons that were breeding

ponds (49.0% correct), and identifying polygons that were not breeding ponds (80.6% correct).

Nearly one-third of the 958 lentic wetlands on the NPS-DEWA datalayer were classified as breeding ponds (n = 308). Cowardin Class and Water Regime Modifier attributes were available for 931 NPS-DEWA wetlands, of which, 304 of them were classified as breeding ponds. Three quarters of OW wetlands (n = 137) were classified as breeding ponds, whereas SS (n = 137) and FO (n = 552) wetlands were 6.7 and 9.7 times less likely, respectively, to be breeding ponds than OW wetlands (Table 4.3). Again, EM wetlands (n = 126) were the least likely to be breeding ponds. As with NWI wetlands, the proportion of NPS-DEWA wetlands classified as breeding ponds did not always increase between each modifier with longer predicted hydroperiods (Table 4.4). Notably, only 8.9% of seasonally flooded wetlands (n = 56) were classified as breeding ponds compared to 20.5% of those classified as intermittently saturated (n = 468), and 44.5% seasonally saturated/flooded wetlands (n = 160). More than half of all wetlands with at least seasonally saturated/flooded hydroperiods were breeding ponds (Table 4.5).

In CART analyses of NPS-DEWA wetlands, Water Regime Modifier was used in primary and secondary splits of the data, whereas wetland size was used in tertiary and quaternary splits (Figure 4.4). A classification tree with seven groupings of wetlands predicted that breeding ponds were among: 1) wetlands with at least semi-permanent hydroperiods, 2) wetlands with seasonally flooded/saturated hydroperiods and smaller than 0.13 ha, and 3) wetlands with temporarily flooded and intermittently saturated wetlands at least 5.8 ha in size. This classification tree had an overall misclassification rate of 22.9%, identified 92.2% of wetland polygons that were not breeding ponds, but identify less than half (46.1%) of breeding ponds. Using Class to categorize breeding ponds had a similar overall misclassification rate (23.9%), it identified 94.7% of non-breeding pond wetland polygons, and identified only 33.2% of breeding ponds.

LiDAR Model Predictions

Of the 24 LiDAR ponds, eight were included on the NWI datalayer, and there was no significant difference in size between LiDAR ponds included on the NWI datalayer (mean = 0.21 ha, median = 0.13 ha, StDev = 0.20) and those that were not included (mean = 0.24 ha, median = 0.13 ha, StDev = 0.24) (Kruskal-Wallis test, $H = 0.00$, $DF = 1$, $P = 0.951$). Concordance scores were slightly higher, and sensitivity scores were slightly lower, for LiDAR ponds included on the NWI datalayer than those that were not included (Table 4.6), but neither of these differences were statistically significant (Concordance, $H = 0.74$, $DF = 1$, $P = 0.391$; Sensitivity, $H = 0.74$, $DF = 1$, $P = 0.391$). Therefore, LiDAR models perform equally well for ponds detected by NWI as they do for undetected ponds when discriminating between flooded and upland habitats (concordance), and when classifying known areas of standing water (sensitivity). Compared to other accuracy measures, the difference in specificity scores between included and non-included ponds was relatively large. More upland habitat was incorrectly classified among LiDAR ponds not included on the NWI datalayer, than among LiDAR ponds included on the NWI datalayer, although this difference was not statistically significant ($H = 2.54$, $DF = 1$, $P = 0.111$).

A total of 16 LiDAR ponds were included on the NPS datalayer and those ponds were larger in size (mean = 0.29 ha, median = 0.19 ha, StDev = 0.23) than the eight LiDAR ponds that were not included on the NPS datalayer (mean = 0.05 ha, median = 0.04 ha, StDev = 0.04) ($H = 8.60$, $DF = 1$, $P = 0.003$). LiDAR models were typically more accurate among ponds included on the NPS datalayer than among those not included (Table 4.7), but these differences were not statistically significant for any measure of accuracy (Concordance, $H = 0.64$, $DF = 1$, $P = 0.424$; Sensitivity, $H = 0.22$, $DF = 1$, $P = 0.641$; Specificity, $H = 2.35$, $DF = 1$, $P = 0.125$). Similar to the NWI datalayer, specificity was the accuracy measure that displayed the greatest differences between ponds included on the NPS datalayer and those not included, but this difference was not statistically significant.

DISCUSSION

Breeding Pond Size and Occurrence on Wetlands Maps

It is not possible to accurately assess the status and trends of pond-breeding amphibian wetlands using only the NWI database because of its inability to detect small, seasonal wetlands. The NWI datalayer in this study failed to detect the majority of ponds smaller than 0.5 ha, and these ponds likely comprise the majority of breeding sites for nine species of amphibians in the New Jersey portion of the DEWA (Julian et al. Chapter 2). The NWI datalayer potentially could be used to assess changes in amphibian breeding wetland area because undetected breeding ponds account for relatively little cumulative breeding pond area. However, monitoring the number of breeding ponds may be more important than cumulative area because small breeding ponds can produce as many recruits as larger ones (Julian et al. Chapter 2).

The high likelihood that wetlands smaller than 0.5 ha will be omitted from NWI wetland maps leads us to suspect that national trends reported by Dahl (2006) vastly underestimate the rate small wetlands are lost in the landscape relative to larger wetlands. Based on NWI data, Dahl (2006), found the amount of wetland area lost to degradation and destruction among wetlands smaller than 0.5 ha was equivalent to the area lost among larger wetlands. However, our results suggest the amount of small wetland area lost could be more than twice as high as the amount of large wetland area because the rate wetlands < 0.5 ha go undetected on NWI wetland maps is 2.3 times higher than the rate wetlands > 0.5 ha go undetected.

The use of a datalayer based upon 1:12,000 CIR photography would be an improvement over the NWI datalayer because it appears to detect wetlands an order of magnitude smaller with the same level of accuracy. The inability of 1:12,000 CIR photography to map wetlands smaller than 0.1 ha, however, will hamper attempts to assess the status and trends of several amphibian species in forested landscapes across the northeastern U.S. Seasonal and geographically isolated wetlands smaller than 0.1 ha are used heavily by amphibian species that breed in early spring, and half of all geographically isolated wetlands in NJ-DEWA were smaller than 0.1 ha (Julian et al. Chapter 3). Furthermore,

seasonal ponds less than 0.1 ha in size comprised 80% of all seasonal pools identified in the Quabbin Reservoir Watershed, Massachusetts (Brooks et al. 1998), and among several counties in Maine (Calhoun et al. 2003).

The relationship we estimated between pond size and detectability was comparable to relationships inferred in other studies. The likely detection limit of seasonal pools from 1:12,000 CIR aerial photography was estimated to be between 0.005 - 0.01 ha by Burne (2001), which corresponds to detection probabilities of approximately 25 – 35% for ponds of similar size in our study. Although very few breeding ponds in DEWA are < 0.01 ha (approximately 3%), Calhoun et al. (2003) found that up to 80% of seasonal pools Penobscot County were this small. The omission rate of wetlands < 0.2 ha in size from the DEWA-NPS datalayer (28.9%) was similar to the omission rate of similarly-sized seasonal pools from aerial photography of deciduous forests in southern Maine (Calhoun et al. 2003). Calhoun et al. (2003) found that interpretations of aerial photography (at scales as fine as 1:4,800) failed to detect at least 27% of field-validated seasonal ponds (85% which were smaller than 0.2 ha in size). However, they also suggested the detection of small, seasonal ponds via aerial photography is affected more by maximum pond depth and surrounding forest vegetation than pond area.

Size-dependent detection rates that we report could help investigators estimate the amount of small amphibian breeding ponds in their study areas when they are constrained by the use of pre-existing GIS datalayers. Investigators could estimate the total number of small ponds in a study area by dividing the number of small ponds included on a datalayer by the estimated rate of detection. For instance, if field validation of an NWI datalayer indicated a study area contained eight amphibian breeding ponds smaller than 0.5 ha, then detection rates would predict a total of 22 ponds of this size in the study area. This approach may lack the desired rigor to assess status and trends in small wetlands loss, but it could prove useful in establishing goals for programs that intend to locate, inventory, and geo-reference unmapped vernal pools.

Identifying Breeding Ponds Among GIS Wetland Polygons

To identify amphibian breeding ponds among NWI wetlands, investigators should search among wetlands with Water Regime modifiers that are at least temporarily flooded and within FO or OW Classes. CART suggests that Class yielded more accurate predictions of both breeding ponds and non-breeding ponds when it is first placed in the context of suspected hydroperiod, whereas wetlands size was an important predictor only within the context of Class. Therefore, using the decision tree we generated (Figure 4.3) would be a more efficient way of prioritizing NWI wetlands for field validation of amphibian breeding ponds than using Class by itself.

In contrast, the decision tree we generated for the 1:12,000 wetland datalayer (Figure 4.4) primarily used hydroperiod to identify breeding ponds, and failed to produce predictions that were considerably more accurate than using Class alone as a predictor. At this scale of photography, it may be relatively easier to distinguish between in-pond vegetation types than to determine hydroperiod. The distinction between “seasonally flooded/saturated” and “seasonally flooded” appeared uncertain because polygons in the former class were more likely to be breeding ponds than the later (Table 4.4), even though “seasonally flooded/saturated” suggests a shorter hydroperiod. This discrepancy was greater at the 1:12,000 scale of the NPS-DEWA datalayer than on the NWI datalayer, and NPS-DEWA contained an additional discrepancy between “intermittently saturated” and “temporarily flooded” classes.

While our results support assertions that Cowardin open-water wetlands are more likely to be breeding ponds than other wetland classes (Calhoun et al. 2003, Burne and Lathrop 2008), this trend was much less clear for wetland polygons on our NWI datalayer than our datalayer based on 1:12,000 imagery. OW polygons were ≥ 6.4 times more likely to be breeding ponds than other vegetation classes among wetlands on the 1:12,000 datalayer, but only ≥ 3.3 times more likely among wetlands on the NWI datalayer. CART could, however, be useful in identifying breeding ponds on 1:12,000 datalayers that are not classified as OW.

LiDAR Model Predictions

Green-laser LiDAR technology has been successfully used to predict the occurrence of standing water (Julian et al. 2009), and we feel it has the potential to detect more wetlands than either 1:58,000 or 1:12,000 CIR photography because it can predict standing water as accurately for wetlands that are not detected by these methods, as it can for wetlands that are detected. This result is especially encouraging in the context of the DEWA-NPS datalayer because LiDAR ponds not detected on this datalayer were significantly smaller than detected ponds, and there is some evidence that LiDAR predictions are more accurate for larger ponds than smaller ones (Julian et al. 2009). Therefore, we feel the size-related bias of LiDAR predictions observed by Julian et al (2009) is relatively minor in practice when attempting to identify ponds too small to be detected by 1:12,000 CIR photography. LiDAR derived wetland maps could, however, overestimate the amount of flooded wetland area in the landscape, and this potential seems most likely around ponds that are not detected by aerial photography. However, the predictive model we evaluated in this study did not include elevation data collected by this LiDAR array, and the incorporation of these data should further improve predictions of pond boundaries.

In summary, we found that low detection rates of small, seasonal ponds on wetland datalayers based on 1:58,000 and 1:12,000 aerial photography underestimate the number of amphibian breeding wetlands in the landscape, and this can underestimate national trends that express the relative effect of degradation and development on wetlands < 0.5 ha. Initiatives that attempt to verify the locations of seasonal and geographically isolated wetlands (i.e., vernal pools) can use decision trees in a process similar to the one we developed in order to prioritize wetlands for field verification. However, decision trees will likely prove more useful when applied to wetland datalayers based on 1:58,000 than 1:12,000 aerial photography. The use of LiDAR for the detection of small wetlands seems promising because its accuracy does not appear to be compromised among wetlands too small to be detected by a scale of aerial photography (1:12,000) that is deemed appropriate for the effective detection of small, seasonal ponds (Brooks et al. 1998).

Table 4.1. The percent of amphibian breeding ponds in DEWA that were not included (% **undetected**) on: 1) NWI and 2) NPS-DEWA datalayers by size class.

Pond size	No. Breeding ponds	% Undetected	
		NWI	NPS-DEWA
< 0.1 ha	96	87.5%	36.5%
0.1 - 0.5ha	111	43.2%	5.4%
0.5 – 1.0 ha	24	29.2%	4.2%
1.0 – 2.0 ha	22	13.6%	0.0%
> 2.0 ha	23	0.0%	0.0%

Table 4.2. The percent of amphibian breeding ponds in DEWA not included (**undetected**) on: 1) NWI and 2) NPS-DEWA datalayers by cutoff pond sizes.

Cutoff size	% of larger ponds		% of smaller ponds	
	undetected		undetected	
	NWI	NPS-DEWA	NWI	NPS-DEWA
0.1 ha	32.2%	3.9%	87.5%	36.5%
0.5 ha	14.5%	1.4%	63.8%	19.8%
1.0 ha	6.7%	0.0%	60.2%	18.2%
2.0 ha	0.0%	0.0%	56.1%	16.6%
12.0 ha	NA	NA	51.4%	15.2%

Table 4.3. Percent of wetland polygons by Cowardin Class that were amphibian breeding ponds on 1) NWI (N = 317) and 2) NPS-DEWA (N = 931) datalayers.

Cowardin Class	% Breeding ponds	
	NWI	NPS-DEWA
FO	37.0%	24.6%
OW	68.6%	75.9%
SS	39.5%	31.9%
EM	17.4%	21.4%

Table 4.4. Percent of wetland polygons by Water Regime Modifier that were amphibian breeding ponds on the: 1) NWI and 2) NPS-DEWA datalayers.

Water Regime Modifier	NWI		NPS-DEWA	
	No. Wetland polygons	%Breeding ponds	No. Wetland polygons	%Breeding ponds
≤ Intermittently flooded	19	10.5%	470	20.8%
Temporarily flooded	9	44.4%	72	4.2%
Seasonally flooded/saturated	27	55.6%	160	44.4%
Seasonally flooded	6	33.5%	56	8.9%
> Semi-permanently flooded	27	66.5%	173	73.4%

Table 4.5. Proportion of wetland polygons among groupings of Water Regime Modifier that were amphibian breeding ponds on the 1) NWI and 2) NPS-DEWA datalayers.

Minimum Water Regime Modifier	Percent breeding ponds	
	NWI	NPS-DEWA
> Temporarily flooded	56.5%	44.7%
> Seasonally flooded/saturated	58.3%	52.2%
> Seasonally flooded	60.6%	57.6%
> Semi-permanently flooded	66.5%	73.4%

Table 4.6. Measures of LiDAR model accuracy for DEWA breeding ponds that were detected (N = 8) and not detected (N = 16) on the NWI datalayer.

	Concordance		Sensitivity		Specificity	
	Detected	Undetected	Detected	Undetected	Detected	Undetected
Mean	0.863	0.817	0.733	0.775	0.885	0.803
Median	0.875	0.835	0.769	0.774	0.871	0.827
Minimum	0.748	0.565	0.574	0.558	0.825	0.33
Maximum	0.875	0.835	0.862	0.962	0.948	0.984

Table 4.7. Measures of LiDAR model accuracy for DEWA breeding ponds that were detected (N = 16) and not detected (N = 8) on the DEWA-NPS datalayer.

	Concordance		Sensitivity		Specificity	
	Detected	Undetected	Detected	Undetected	Detected	Undetected
Mean	0.842	0.803	0.768	0.739	0.839	0.805
Median	0.838	0.814	0.769	0.74	0.869	0.794
Minimum	0.565	0.654	0.574	0.558	0.33	0.676
Maximum	0.950	0.942	0.962	0.904	0.957	0.984

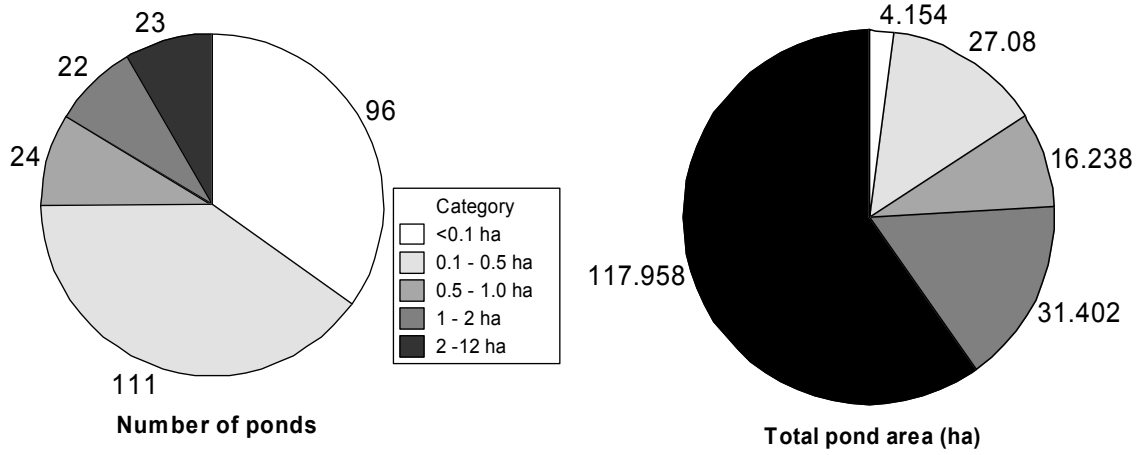


Figure 4.1. Distribution of amphibian breeding ponds in DEWA among size classes by: A) pond abundance and B) cumulative pond area.

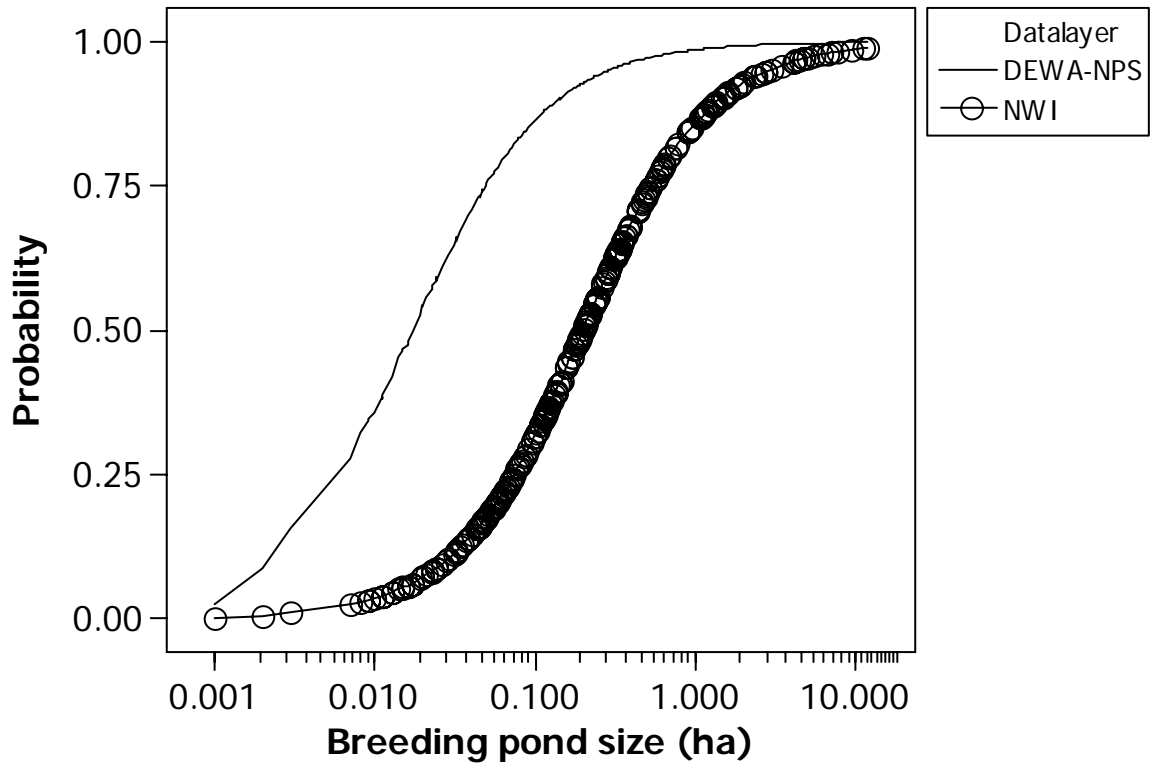


Figure 4.2. Predicted probability a breeding pond in DEWA will be included on the: 1) NWI (probNWI), and 2) NPS-DEWA (probNPS) datalayers as a function of pond size.

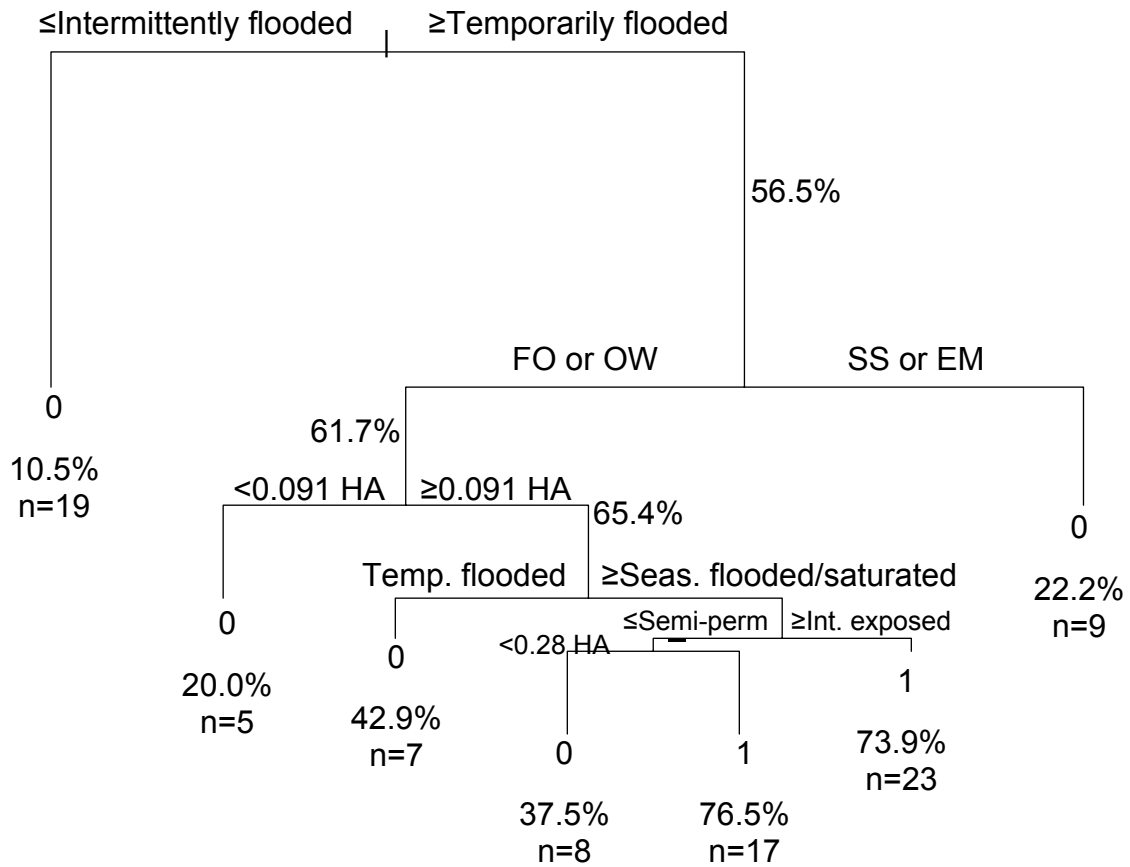


Figure 4.3. CART decision tree for NWI wetland polygons in DEWA. Percentages represent the percent of polygons in that grouping that were breeding ponds. Below terminal nodes; “0” = grouping is predicted to not be breeding ponds, “1” = grouping is predicted to be breeding ponds, “n” = sample size of grouping.

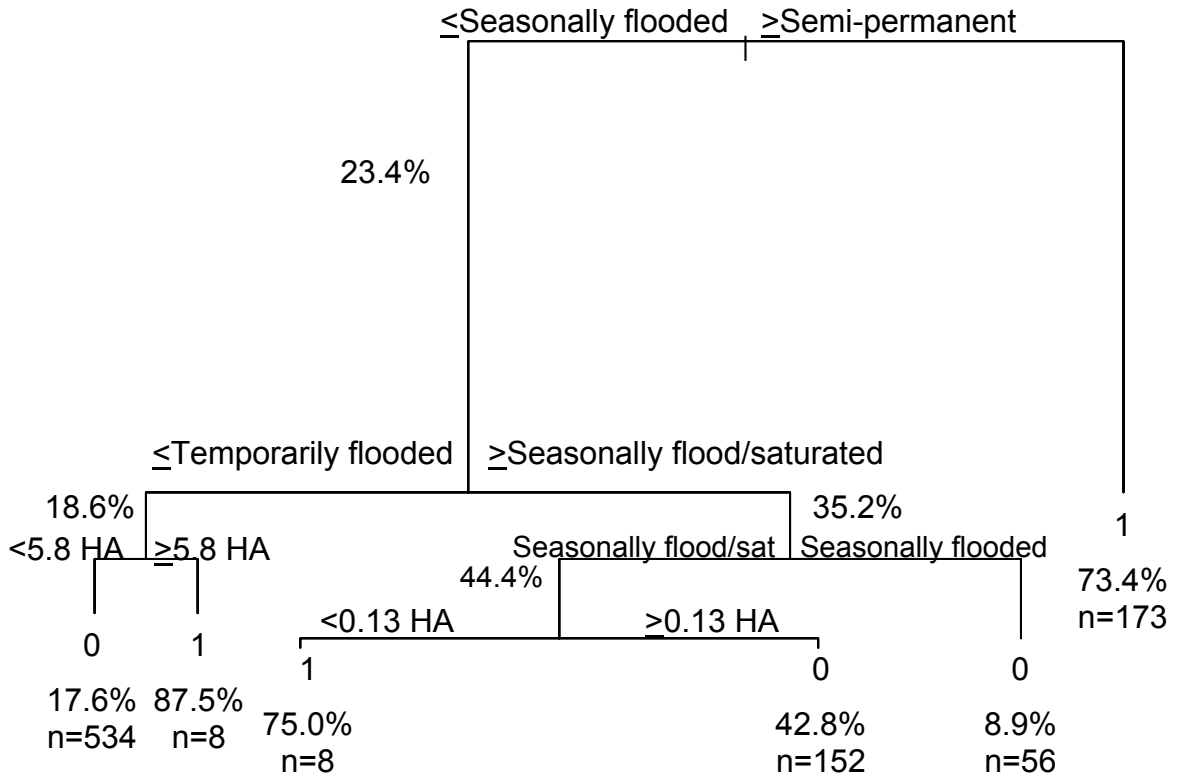


Figure 4.4. CART decision tree for NPS-DEWA wetland polygons in DEWA. Percentages represent the percent of polygons in that grouping that were breeding ponds. Below terminal nodes; “0” = grouping is predicted to not be breeding ponds, “1” = grouping predicted to be breeding ponds, “n” = sample size of grouping.

CONCLUSIONS

It is important to characterize the type of stream connection (i.e., hydrologic connectivity) at a wetland because this attribute is useful in predicting the occurrence patterns of several amphibian species (Julian et al. Chapter 1). Determining whether a wetland lacks a stream connection, contains a seasonal connection, or contains a permanent connection is much less costly in terms of site visits and person hours than determining the presence of fish predators and wetland hydroperiod, both of which are known to influence amphibian species occurrence. Furthermore, hydrologic connectivity is a better predictor of occurrence than fish presence for most amphibian species, even though connectivity is a significant predictor of fish presence. Fish presence may have been a stronger predictor of amphibian occurrence if I took into consideration which fish taxa were present. Different fish taxa could exert varying degrees of predatory pressure on amphibian populations, and this hypothesis could be explored with the data collected in this study. Wetland size had a positive relationship with occurrence for several species, but this relationship needed to be framed within the context of either hydrologic connectivity or the percent of upland forest canopy cover within 250 m of the wetland. Maintaining upland forested habitats is critical to the conservation of many pond-breeding amphibians, and my results seem to concur with this. I did not investigate how directional aspects of upland forested habitat influenced occurrence patterns, but this approach could shed light on the conservation value of maintaining corridors of upland forested habitat that do not completely surround ponds.

The presence of small and isolated wetlands was important in maintaining populations of pond-breeding amphibians across the landscape, especially those of early-breeding species (Julian et al. Chapter 2). Based on species occupancy model predictions, two-thirds of all species contained at least half of their breeding sites in either wetlands that lack permanent stream connections, or wetlands < 0.3 ha in size. In addition, the loss of wetlands < 0.3 ha in size would triple inter-pond dispersal distances, resulting in a landscape that would reduce the likelihood of colonization at unoccupied wetlands. Unfortunately, small and isolated wetlands are rarely protected by federal and state legislation, and federal agencies do not assess their abundance when reporting national

trends in wetland losses. My research illustrates the importance of preserving these wetlands in order to maintain amphibian diversity across the landscape, as well as the importance of inventorying these wetlands to assess potential impacts on amphibian diversity that result from the destruction and degradation of wetlands. Some states have adopted legislation that protects isolated wetlands, but typically these laws only protect upland habitat within 30 m of the wetland's flooded perimeter. A future direction of this work could include modeling changes in amphibian occupancy patterns as a result of the development of upland forest beyond 30 m from the wetland's perimeter.

Amphibian assemblages (Julian et al. Chapter 2) and hydrologic characteristics (Julian et al. Chapter 3) of wetlands varied across gradients of hydrologic connectivity, suggesting that wetlands which lack stream connections function differently than those with seasonal connections. Including both of these wetland types in the jurisdictional definition of an isolated wetland is commonplace, and may be an effective means of protecting both of these wetland types. However, grouping them together can make it more difficult to predict hydroperiod, water chemistry, and the amphibian species they contain. Therefore, attempts to predict ecological functions of isolated wetlands should consider whether a wetland contains a seasonal stream connection in order to provide a more thorough assessment of its conservation value.

In landscapes similar to our study area, the threat of losing breeding populations via habitat destruction is much greater for early-breeding species than species that breed later in the year because the majority of wetlands in NJ-DEWA were small (< 0.5 ha) and isolated (Julian et al. Chapter 3). Small (< 0.5 ha) amphibian breeding wetlands are likely to be degraded and destroyed at much greater rates (up to 21 times) than larger breeding wetlands. This is because small wetlands were three times more abundant than larger wetlands while accounting for only 15% of the total wetland area and the loss of wetlands < 0.5 ha likely accounts for half of all wetland area lost nationally (Dahl 2006). Furthermore, this disparity in the number of wetlands lost could be twice as large because the rate at which small wetlands in my study area were detected on National Wetland Inventory wetland maps (NWI, <http://www.nwi.fws.gov>) was considerably lower than

detection rates for larger wetlands (Julian et al. Chapter 4). The identification of small wetlands in the landscape can be markedly improved by using wetland maps based on 1:12,000 aerial photography because these maps can detect wetlands an order of magnitude smaller than NWI wetland maps with similar detection rates. Although wetland maps based on 1:12,000 aerial photography can still omit 1/3 of wetlands smaller than 0.1 ha, investigators could use estimates of size-dependent detection rates to estimate the number of small-sized wetlands in their study area. This would enable investigators to better plan field-efforts to locate, map, and inventory these small, isolated wetlands. Finally, I found that predictions of the flooded areas of ponds by an airborne light detecting and ranging (LiDAR) sensor were just as accurate for ponds detected on wetland maps as those that were not detected. This suggests that LiDAR technology could be used as a means to effectively map small wetlands that are not readily detected with aerial photography.

APPENDIX A: SUPPLEMENTAL DATA

Appendix A.1. Site characteristics used in occupancy models and the calculation of spatial isolation metrics for all potential amphibian breeding wetlands in NJ-DEWA.

Site	Connect¹	Area² (ha)	P25³	P250⁴	MinDist⁵ (m)	Ponds1km⁶	Area1km⁷ (ha)
122	Seasonal	0.017	1.000	0.733	322	1	0.060
151	Isolated	0.176	0.000	0.283	1032	0	0.000
209	Seasonal	0.062	1.000	0.841	332	2	0.067
210	Seasonal	0.023	1.000	1.000	65	4	0.681
228	Isolated	0.316	0.788	0.829	73	12	6.782
232	Seasonal	0.204	1.000	0.870	162	12	11.645
238	Seasonal	1.227	1.000	1.000	151	12	10.557
245	Isolated	0.134	0.991	1.000	244	9	5.702
248	Permanent	0.074	0.393	0.504	38	11	7.047
271	Permanent	1.334	0.000	0.298	21	12	5.801
302	Permanent	1.271	0.000	0.135	476	1	0.013
310	Permanent	0.013	1.000	0.686	476	1	1.271
362	Isolated	0.194	0.948	0.651	55	5	2.759
367	Permanent	2.25	0.470	0.810	55	7	2.830
374	Isolated	0.124	1.000	0.915	123	5	4.840
402	Isolated	0.111	0.856	0.319	407	6	3.022
406	Seasonal	0.047	0.762	0.841	296	4	0.529
419	Isolated	0.067	0.944	0.710	14	4	0.509
420	Isolated	0.294	1.000	0.726	14	4	0.282
429	Permanent	2.016	0.503	0.955	10	6	9.455
435	Permanent	0.038	0.913	0.936	10	3	6.324
464	Isolated	0.217	1.000	0.760	171	6	14.086
483	Permanent	0.118	0.829	0.659	45	2	6.989
494	Seasonal	0.056	1.000	0.945	221	6	13.403
498	Permanent	7.744	0.732	0.940	94	6	5.715
508	Isolated	0.141	1.000	0.981	94	6	13.317
517	Permanent	0.054	0.553	0.806	85	7	9.644
532	Permanent	1.156	0.516	0.800	85	7	8.542
541	Seasonal	0.002	1.000	1.000	318	3	3.588
564	Permanent	0.441	0.249	0.698	167	3	1.314
569	Permanent	0.104	0.738	0.483	167	4	1.776
600	Isolated	0.12	0.996	0.716	876	2	2.452
611	Isolated	0.125	0.000	0.260	903	3	0.184
625	Permanent	0.074	0.102	0.742	476	2	0.201
632	Permanent	0.081	0.000	0.502	476	3	0.150
647	Seasonal	0.058	1.000	0.833	33	17	2.415
651	Isolated	0.043	1.000	0.886	70	16	2.305
656	Seasonal	1.232	0.464	0.393	7	18	1.543
663	Seasonal	0.028	0.279	0.443	11	18	2.747
666	Seasonal	0.089	0.515	0.234	5	18	2.686
667	Seasonal	0.243	0.990	0.948	354	4	6.132
668	Permanent	1.278	0.541	0.931	92	6	7.496
676	Permanent	0.238	0.057	0.453	324	10	1.861
684	Seasonal	0.234	0.817	0.604	147	7	0.601
688	Isolated	0.333	0.967	0.997	10	17	2.204
689	Seasonal	0.264	0.298	0.512	147	6	0.780
694	Isolated	0.09	0.953	0.996	10	16	2.424
697	Isolated	0.077	0.930	0.996	75	16	2.437

Site	Connect ¹	Area ² (ha)	P25 ³	P250 ⁴	MinDist ⁵ (m)	Ponds1km ⁶	Area1km ⁷ (ha)
698	Isolated	0.044	1.000	0.995	28	15	2.429
699	Permanent	1.312	0.719	0.968	206	5	6.137
704	Isolated	0.189	0.950	0.999	358	14	7.125
710	Permanent	0.064	0.858	0.957	266	6	8.711
716	Seasonal	0.197	1.000	0.929	470	5	0.832
741	Isolated	0.698	0.549	0.898	815	1	1.075
743	Permanent	1.6	1.000	0.973	29	4	17.425
751	Isolated	0.006	1.000	1.000	631	5	0.918
758	Isolated	0.357	0.445	0.633	256	8	1.126
764	Seasonal	0.33	1.000	1.000	206	2	3.228
775	Seasonal	0.508	1.000	0.960	206	3	3.512
787	Isolated	0.032	0.504	0.725	229	2	0.113
799	Isolated	0.009	1.000	0.428	55	11	5.133
800	Isolated	0.38	0.897	0.387	52	11	4.762
801	Isolated	0.752	0.838	0.986	106	16	4.561
803	Isolated	0.162	0.990	0.995	263	9	35.197
807	Seasonal	1.489	0.751	0.349	5	10	3.543
808	Isolated	0.935	0.211	0.219	5	10	4.097
810	Isolated	0.079	0.875	0.989	127	14	5.027
816	Isolated	0.429	0.945	0.995	145	7	26.691
818	Permanent	6.064	0.667	0.942	254	1	0.120
819	Isolated	0.219	1.000	0.930	232	13	5.569
823	Permanent	0.42	0.962	0.944	120	7	22.400
835	Seasonal	0.757	1.000	0.690	466	7	3.399
837	Seasonal	0.12	1.000	0.999	254	1	6.064
845	Seasonal	0.387	0.384	0.834	213	2	0.064
870	Seasonal	0.145	0.910	0.997	222	2	11.287
905	Permanent	0.484	0.005	0.902	998	1	0.681
961	Permanent	2.324	0.035	0.635	20	9	2.128
962	Permanent	0.086	0.832	0.673	12	8	4.225
963	Permanent	1.081	0.503	0.590	10	8	3.230
966	Permanent	0.221	0.124	0.632	20	10	4.271
968	Permanent	0.221	0.177	0.597	12	8	4.090
971	Permanent	0.116	0.137	0.638	56	8	4.195
973	Isolated	0.141	0.933	0.998	241	5	2.766
977	Isolated	0.05	1.000	1.000	420	11	4.573
986	Isolated	0.04	1.000	0.899	241	4	0.543
995	Seasonal	0.079	0.761	0.540	526	3	0.773
1001	Isolated	0.321	0.988	0.946	26	2	6.256
1011	Permanent	0.168	0.677	0.481	115	4	0.926
1015	Permanent	0.317	0.105	0.374	115	4	0.777
1038	Seasonal	0.243	0.393	0.543	341	3	0.773
1042	Seasonal	0.779	0.831	0.967	213	3	5.009
1051	Isolated	0.507	0.810	0.933	213	3	5.282
1084	Permanent	9.357	0.598	0.935	444	2	0.417
1086	Isolated	0.066	0.610	0.805	559	1	9.357
1091	Seasonal	0.352	0.600	0.815	444	3	9.716
1096	Seasonal	0.273	0.301	0.363	45	2	0.314
1101	Seasonal	0.296	0.993	0.780	113	2	0.415
2012	Isolated	0.045	1.000	1.000	65	5	0.792
2025	Isolated	0.137	0.857	0.688	256	10	2.125
2026	Permanent	0.11	0.547	0.926	268	14	3.083
2027	Isolated	0.045	0.794	0.548	165	11	4.367
2028	Isolated	0.026	0.840	0.955	96	11	2.420

Site	Connect ¹	Area ² (ha)	P25 ³	P250 ⁴	MinDist ⁵ (m)	Ponds1km ⁶	Area1km ⁷ (ha)
2029	Isolated	0.054	1.000	0.711	95	10	4.978
2030	Isolated	0.011	1.000	0.984	213	2	0.440
2031	Isolated	0.053	1.000	1.000	346	2	0.398
2032	Seasonal	0.02	1.000	0.998	222	4	0.232
2033	Isolated	0.131	0.789	0.837	303	3	0.231
2034	Permanent	4.492	0.668	0.950	370	5	3.383
2036	Seasonal	0.064	0.990	0.595	113	2	0.648
3004	Isolated	0.011	1.000	0.950	370	3	5.778
3006	Seasonal	0.082	0.000	0.317	229	2	0.505
3007	Isolated	0.071	0.020	0.608	294	8	2.077
3009	Permanent	0.107	0.792	0.731	229	6	1.195
3010	Isolated	0.619	0.961	0.937	8	12	2.248
3011	Seasonal	0.232	0.005	0.326	45	2	0.356
3012	Isolated	0.258	0.974	0.911	73	12	6.840
3013	Seasonal	0.013	0.980	1.000	151	11	11.703
3014	Seasonal	0.028	0.407	0.225	135	17	2.725
3015	Isolated	0.038	0.950	0.589	49	18	2.737
3016	Isolated	0.074	0.000	0.495	29	18	2.701
3018	Isolated	0.057	0.945	0.706	172	4	0.519
3019	Seasonal	0.052	1.000	1.000	164	6	0.403
3020	Isolated	0.017	1.000	1.000	138	7	0.819
3022	Isolated	0.044	1.000	0.925	8	10	2.290
3023	Seasonal	0.038	1.000	0.724	49	17	2.548
3024	Isolated	0.024	1.000	1.000	164	5	0.398
3027	Isolated	0.031	1.000	0.996	61	9	2.197
3031	Seasonal	0.034	0.000	0.446	51	1	0.115
4005	Isolated	0.032	1.000	1.000	271	6	0.779
4007	Isolated	0.015	1.000	0.979	138	6	0.624
5001	Permanent	0.034	0.000	0.145	21	12	7.101
5002	Seasonal	0.023	0.944	0.841	33	13	2.212
5003	Isolated	0.008	0.809	0.812	82	16	2.340
5004	Seasonal	0.041	0.000	0.408	122	17	2.690
5006	Seasonal	0.103	0.555	0.311	5	18	2.672
5011	Seasonal	0.461	0.845	0.949	146	9	29.363
5012	Permanent	3.478	0.357	0.939	92	6	5.296
5014	Permanent	1.765	0.763	0.943	26	2	4.813
5015	Permanent	0.953	0.042	0.499	52	2	0.277
5016	Permanent	1.075	0.685	0.963	84	6	8.155
5017	Permanent	0.056	0.499	0.627	10	8	4.255
5019	Seasonal	0.04	0.024	0.893	31	7	0.108
5020	Seasonal	0.022	0.000	0.891	25	7	0.125
5021	Seasonal	0.025	0.030	0.891	25	7	0.123
5022	Isolated	0.01	0.022	0.888	20	6	0.118
5023	Seasonal	0.015	0.017	0.889	22	5	0.101
5024	Isolated	0.004	0.566	0.886	26	6	0.124
5025	Permanent	0.012	0.000	0.889	20	5	0.101
5026	Isolated	0.073	0.865	0.380	244	5	2.879
6001	Permanent	4.728	0.673	0.946	300	7	1.897
6005	Permanent	0.273	0.103	0.528	52	2	0.958
6007	Seasonal	2.736	0.667	0.344	13	3	6.388
6008	Seasonal	4.254	0.374	0.544	13	2	2.854
6013	Seasonal	2.378	0.406	0.882	318	2	0.123
6019	Permanent	1.325	0.633	0.953	84	4	5.895
6020	Seasonal	0.285	0.526	0.658	503	3	0.467

Site	Connect ¹	Area ² (ha)	P25 ³	P250 ⁴	MinDist ⁵ (m)	Ponds1km ⁶	Area1km ⁷ (ha)
6021	Permanent	4.708	0.807	0.971	29	4	14.045
6022	Permanent	5.52	0.728	0.968	360	7	23.407
6023	Seasonal	2.72	0.557	0.896	146	8	25.405
6024	Isolated	6.735	0.360	0.868	47	11	34.933
6025	Isolated	7.019	0.705	0.904	47	6	24.739
6026	Seasonal	0.313	0.000	0.574	200	13	5.475
6028	Permanent	11.267	0.520	0.920	120	9	18.718
6029	Isolated	0.625	0.828	0.977	317	6	26.033
6032	Permanent	0.681	0.120	0.899	47	2	0.587
6033	Permanent	0.103	0.494	0.866	47	1	0.681
6035	Permanent	0.157	0.000	0.770	111	8	4.154
6036	Permanent	0.287	0.263	0.800	320	4	0.808
6037	Seasonal	0.115	0.008	0.450	51	1	0.034
6040	Permanent	4.091	0.281	0.595	171	6	10.212
6042	Permanent	0.223	0.670	0.522	68	10	6.808
6043	Permanent	3.214	0.170	0.464	38	12	3.921
7004	Permanent	0.06	0.577	0.321	322	2	0.184
7022	Permanent	0.005	0.000	0.449	480	6	4.049
7023	Permanent	0.307	0.447	0.644	480	6	2.756

¹Connect: strictly isolated=Isolated, seasonal connection=Seasonal, permanent connection= Permanent

²Area: wetland area

³P25: proportion of forested area within 25 m of flooded perimeter with > 50% canopy cover

⁴P250: proportion of forested area within 250 m of flooded perimeter with > 50% canopy cover

⁵MinDist: distance to nearest potential amphibian breeding wetland

⁶Ponds1km: number of potential amphibian breeding wetlands within 1 km of flooded perimeter

⁷Area1km: total area of potential amphibian breeding wetlands within 1 km of flooded perimeter

Appendix A.2. Species encountered (0 = never encountered, 1 = encountered at least once) during amphibian surveys at sites in New Jersey (NJ) and Pennsylvania (PA) in DEWA (AMAC *A. maculatum*, BUFO *Bufo* species, HVER *H. versicolor*, NVIR *N. viridescens*, PCRU *P. crucifer*, RCAT *R. catesbeiana*, RCCU *R. clamitans*, RPAL *R. palustris*, RSYL *R. sylvatica*).

Site	State	AMAC	BUFO	HVER	NVIR	PCRU	RCAT	RCLA	RPAL	RSYL
122	NJ	0	0	0	0	0	0	0	0	1
232	NJ	1	0	0	0	0	0	0	0	1
271	NJ	1	1	0	1	1	1	1	1	1
302	NJ	1	0	1	1	1	1	1	1	1
367	NJ	1	0	1	1	1	0	1	0	1
429	NJ	1	0	0	1	1	0	1	0	1
435	NJ	1	0	0	1	1	0	1	0	1
494	NJ	1	0	0	0	0	0	0	0	1
517	NJ	1	0	1	1	1	0	1	1	0
569	NJ	0	0	0	0	0	0	0	1	0
625	NJ	0	1	1	1	0	0	1	0	0
667	NJ	1	0	0	0	0	0	0	0	1
668	NJ	1	0	0	1	1	1	1	0	0
684	NJ	0	0	0	0	0	0	0	0	1
694	NJ	1	0	0	0	0	0	0	0	1
758	NJ	1	0	0	0	0	0	0	0	1
787	NJ	1	0	0	0	0	0	0	0	0
816	NJ	1	0	0	0	0	0	0	0	1
818	NJ	1	0	0	1	1	1	1	1	0
870	NJ	1	0	0	0	1	0	0	0	1
905	NJ	1	0	1	1	1	1	1	1	0
963	NJ	0	1	0	0	0	1	1	1	0
968	NJ	1	1	0	1	1	1	1	1	0
1011	NJ	0	0	0	0	1	1	1	1	0
1086	NJ	0	0	0	0	0	0	0	0	1
1096	NJ	1	1	0	0	0	1	1	1	1
2025	NJ	1	0	0	0	0	0	0	0	1
2026	NJ	1	0	1	1	1	0	1	1	1
2031	NJ	1	0	0	0	0	0	0	0	1
2032	NJ	1	0	0	0	0	0	0	0	1
2034	NJ	1	0	1	1	1	1	1	1	1
3010	NJ	1	0	1	1	1	0	1	0	1
3013	NJ	1	0	0	0	0	0	0	0	1
3018	NJ	1	0	0	0	0	0	0	0	1
3019	NJ	1	0	0	0	0	0	1	0	1
3024	NJ	0	0	0	0	0	0	0	0	0
5002	NJ	1	0	0	0	0	0	1	0	1
6001	NJ	1	0	0	1	1	1	1	1	0
6008	NJ	1	0	0	1	1	1	1	1	0
6019	NJ	1	0	0	0	0	1	1	1	0
6022	NJ	1	1	0	1	0	1	1	0	0
6023	NJ	1	0	1	1	1	0	1	1	0
6037	NJ	1	1	0	0	1	0	1	1	1
6040	NJ	1	0	1	1	1	1	1	1	1
83	PA	1	0	1	1	1	0	1	0	1
129	PA	0	0	0	0	0	0	0	0	0

Site	State	AMAC	BUFO	HVER	NVIR	PCRU	RCAT	RCLA	RPAL	RSYL
131	PA	0	0	0	0	1	0	0	1	1
144	PA	0	0	0	0	0	0	0	0	1
216	PA	1	1	0	0	1	0	1	0	1
254	PA	1	0	0	1	1	0	0	0	1
277	PA	0	0	1	0	0	0	0	0	1
279	PA	1	1	1	0	1	0	1	0	1
309	PA	1	0	1	0	1	0	0	0	1
338	PA	0	1	1	0	1	0	0	1	1
352	PA	1	0	0	0	0	0	0	0	1
355	PA	1	0	0	1	0	1	1	0	1
387	PA	1	0	1	0	1	1	1	0	1
434	PA	1	0	0	0	0	0	0	0	1
664	PA	1	0	0	1	0	0	0	0	0
888	PA	1	0	0	0	0	0	0	0	1
889	PA	0	0	1	0	0	0	0	0	0
890	PA	1	0	1	1	1	0	1	0	1
898	PA	1	0	1	1	1	0	1	1	1
992	PA	1	0	0	1	1	0	1	0	1
1235	PA	1	0	0	0	0	0	0	0	1
1292	PA	1	0	0	0	0	0	0	0	0
2003	PA	1	0	1	0	1	0	1	0	0
2004	PA	1	0	1	1	1	0	1	0	0
2007	PA	1	0	0	0	0	0	0	0	0
2014	PA	0	0	0	0	0	0	0	0	0
5009	PA	0	0	0	0	0	0	0	0	0
6004	PA	0	1	0	1	1	1	1	1	0
6011	PA	1	0	1	1	1	1	1	1	1
6018	PA	1	0	1	1	1	1	1	1	0
6031	PA	0	1	0	1	0	1	1	1	1
6038	PA	1	0	1	1	1	0	1	1	1

Appendix A.3. Encounter histories of *A. maculatum* used in occupancy models by sampling week and site in NJ-DEWA in 2005 (0 = not encountered, 1 = encountered, - = not surveyed).

Site	Primary survey method and sampling week							
	Visual encounter survey			Larval dipnet survey				
	10-Apr	17-Apr	8-May	15-May	12-Jun	19-Jun	10-Jul	17-Jul
122	0	-	0	0	-	-	0	-
232	1	-	1	0	-	-	-	-
271	1	1	1	1	0	0	0	0
302	1	1	0	0	0	0	0	0
367	1	1	1	1	1	1	1	1
429	1	1	1	1	1	1	0	0
435	1	-	1	1	1	1	1	1
494	1	-	1	-	0	-	-	-
517	0	-	0	0	1	1	0	1
569	0	-	0	0	0	0	0	0
625	0	-	0	0	0	-	0	-
667	1	-	1	0	1	1	1	-
668	1	1	1	0	1	1	0	0
684	0	-	0	-	-	-	-	-
694	1	-	1	1	-	-	-	-
758	1	-	1	1	-	-	-	-
787	1	-	1	1	0	-	0	-
816	1	-	1	1	-	-	-	-
818	1	1	1	1	0	0	0	0
870	1	1	1	1	1	1	-	-
905	1	1	1	0	1	1	0	0
963	0	-	0	0	0	-	0	-
968	1	-	1	0	1	0	0	-
1011	0	0	0	0	0	0	0	0
1086	0	-	0	0	-	-	-	-
1096	1	-	1	0	0	0	0	0
2025	1	1	1	-	-	-	-	-
2026	1	1	1	0	1	0	0	0
2031	1	1	1	-	-	-	-	-
2032	1	1	1	1	1	-	-	-
2034	1	-	1	1	0	-	0	-
3010	1	-	1	0	1	-	1	-
3013	1	-	1	1	0	1	1	0
3018	1	-	1	0	0	0	0	0
3019	1	-	1	1	1	-	0	-
3024	0	-	0	-	-	-	-	-
5002	1	0	1	0	0	-	-	-
6001	1	1	1	0	0	0	0	0
6008	1	-	1	0	0	-	0	-
6019	1	1	1	1	0	0	0	0
6022	1	-	0	0	0	-	0	-
6023	1	-	1	1	1	-	1	-
6037	1	1	1	1	1	-	-	-
6040	1	1	1	1	0	0	1	0

Appendix A.4. Encounter histories of *Bufo* species used in occupancy models by sampling week and site in NJ-DEWA in 2005 (0 = not encountered, 1 = encountered, - = not surveyed).

Site	Primary survey method and sampling week				
	Visual encounter survey	Larval dipnet survey			
	8-May	15-May	12-Jun	19-Jun	10-Jul
122	0	0	-	-	0
232	0	0	-	-	-
271	0	1	0	0	0
302	0	0	0	0	0
367	0	0	0	0	0
429	0	0	0	0	0
435	0	0	0	0	0
494	0	-	0	-	-
517	0	0	0	0	0
569	0	0	0	0	0
625	1	1	1	-	0
667	0	0	0	0	0
668	0	0	0	0	0
684	0	-	-	-	-
694	0	0	-	-	-
758	0	0	-	-	-
787	0	0	0	-	0
816	0	0	-	-	-
818	0	0	0	0	0
870	0	0	0	0	-
905	0	0	0	0	0
963	0	0	0	-	1
968	0	1	0	0	0
1011	0	0	0	0	0
1086	0	0	-	-	-
1096	1	1	0	1	0
2025	0	-	-	-	-
2026	0	0	0	0	0
2031	0	-	-	-	-
2032	0	0	0	-	-
2034	0	0	0	-	0
3010	0	0	0	-	0
3013	0	0	0	0	0
3018	0	0	0	0	0
3019	0	0	0	-	0
3024	0	-	-	-	-
5002	0	0	0	-	-
6001	0	0	0	0	0
6008	0	0	0	-	0
6019	0	0	0	0	0
6022	0	0	0	-	1
6023	0	0	0	-	0
6037	0	1	0	-	-
6040	0	0	0	0	0

Appendix A.5. Encounter histories of *Hyla versicolor* used in occupancy models by sampling week and site in NJ-DEWA in 2005 (0 = not encountered, 1 = encountered, - = not surveyed).

Site	Larval dipnet survey				
	15-May	12-Jun	19-Jun	10-Jul	17-Jul
122	-	-	-	0	-
232	0	-	-	-	-
271	0	0	0	0	0
302	0	0	0	1	1
367	0	0	0	0	1
429	0	0	0	0	0
435	0	0	0	0	0
494	0	0	-	-	-
517	0	0	0	1	0
569	0	0	0	0	0
625	0	0	-	1	-
667	0	0	0	0	-
668	0	0	0	0	0
684	0	-	-	-	-
694	0	-	-	-	-
758	0	-	-	-	-
787	0	0	-	0	-
816	0	-	-	-	-
818	0	0	0	0	0
870	0	0	0	-	-
905	0	0	0	1	1
963	0	0	-	0	-
968	0	0	0	0	-
1011	0	0	0	0	0
1086	0	-	-	-	-
1096	0	0	0	0	0
2025	0	-	-	-	-
2026	0	0	1	1	1
2031	0	-	-	-	-
2032	0	0	-	-	-
2034	0	0	-	1	-
3010	0	1	-	1	-
3013	0	0	0	0	0
3018	0	0	0	0	0
3019	0	0	-	0	-
3024	0	-	-	-	-
5002	0	0	-	-	-
6001	0	0	0	0	0
6008	0	0	-	0	-
6019	0	0	0	0	0
6022	0	0	-	0	-
6023	0	0	-	1	-
6037	0	0	-	-	-
6040	0	0	0	1	0

Appendix A.6. Encounter histories of *Notophthalmus viridescens* used in occupancy models by sampling week and site in NJ-DEWA in 2005 (0 = not encountered, 1 = encountered, - = not surveyed).

Site	Larval dipnet survey			
	12-Jun	19-Jun	10-Jul	17-Jul
122	-	-	0	-
232	0	-	-	-
271	0	1	1	1
302	0	1	1	1
367	1	1	1	1
429	1	1	1	1
435	0	0	1	1
494	0	-	-	-
517	0	1	1	1
569	0	0	0	0
625	0	-	1	-
667	0	0	0	-
668	1	0	0	0
684	0	-	-	-
694	0	-	-	-
758	0	-	-	-
787	0	-	0	-
816	0	-	-	-
818	1	0	1	1
870	0	0	-	-
905	1	1	1	0
963	0	-	0	-
968	0	0	1	-
1011	0	0	0	0
1086	0	-	-	-
1096	0	0	0	0
2025	0	-	-	-
2026	0	0	1	0
2031	0	-	-	-
2032	0	-	-	-
2034	0	-	1	-
3010	0	-	1	-
3013	0	0	0	0
3018	0	0	0	0
3019	0	-	0	-
3024	0	-	-	-
5002	0	-	-	-
6001	1	1	1	1
6008	1	-	1	-
6019	0	0	0	0
6022	0	-	1	-
6023	1	-	1	-
6037	0	-	-	-
6040	1	1	1	0

Appendix A.7. Encounter histories of *Pseudacris crucifer* used in occupancy models by sampling week and site in NJ-DEWA in 2005 (0 = not encountered, 1 = encountered, - = not surveyed).

Site	Larval dipnet survey				
	15-May	12-Jun	19-Jun	10-Jul	17-Jul
122	0	-	-	0	-
232	0	-	-	-	-
271	1	1	1	1	0
302	1	1	1	1	1
367	0	1	1	1	1
429	1	1	1	0	0
435	0	1	0	0	0
494	-	0	-	-	-
517	0	1	1	1	1
569	0	0	0	0	0
625	0	0	-	0	-
667	0	0	0	0	-
668	1	0	1	1	1
684	0	-	-	-	-
694	0	-	-	-	-
758	0	-	-	-	-
787	0	0	-	0	-
816	0	-	-	-	-
818	1	1	1	0	0
870	0	1	1	-	-
905	1	1	1	0	0
963	0	0	-	0	-
968	0	1	0	0	-
1011	0	0	0	0	1
1086	0	-	-	-	-
1096	0	0	0	0	0
2025	0	-	-	-	-
2026	0	0	0	0	1
2031	0	-	-	-	-
2032	0	0	-	-	-
2034	0	1	-	1	-
3010	1	1	-	1	-
3013	0	0	0	0	0
3018	0	0	0	0	0
3019	0	0	-	0	-
3024	0	-	-	-	-
5002	0	0	-	-	-
6001	1	1	1	1	0
6008	1	1	-	0	-
6019	0	0	0	0	0
6022	0	0	-	0	-
6023	0	1	-	0	-
6037	0	1	-	-	-
6040	1	1	1	0	0

Appendix A.8. Encounter histories of *Rana catesbeiana* used in occupancy models by sampling week and site in NJ-DEWA in 2005 (0 = not encountered, 1 = encountered, - = not surveyed).

Site	Primary survey method and sampling week						
	Visual encounter survey		Larval dipnet survey				
	10-Apr	8-May	15-May	12-Jun	19-Jun	10-Jul	17-Jul
122	0	0	0	-	-	0	-
232	0	0	0	-	-	-	-
271	0	0	0	0	1	1	1
302	0	0	1	0	1	1	0
367	0	0	0	0	0	0	0
429	0	0	0	0	0	0	0
435	0	0	0	0	0	0	0
494	0	0	-	0	-	-	-
517	0	0	0	0	0	0	0
569	0	0	0	0	0	0	0
625	0	0	0	0	-	0	-
667	0	0	0	0	0	0	-
668	0	0	0	1	0	0	0
684	0	0	-	-	-	-	-
694	0	0	0	-	-	-	-
758	0	0	0	-	-	-	-
787	0	0	0	0	-	0	-
816	0	0	0	-	-	-	-
818	0	1	0	1	1	0	0
870	0	0	0	0	0	-	-
905	0	1	1	0	0	1	0
963	0	0	1	0	-	0	-
968	1	0	0	0	1	0	-
1011	0	0	1	1	1	1	1
1086	0	0	0	-	-	-	-
1096	0	0	0	0	1	0	0
2025	0	0	-	-	-	-	-
2026	0	0	0	0	0	0	0
2031	0	0	-	-	-	-	-
2032	0	0	0	0	-	-	-
2034	0	0	0	1	-	0	-
3010	0	0	0	0	-	0	-
3013	0	0	0	0	0	0	0
3018	0	0	0	0	0	0	0
3019	0	0	0	0	-	0	-
3024	0	0	-	-	-	-	-
5002	0	0	0	0	-	-	-
6001	0	0	0	1	1	0	1
6008	0	0	0	1	-	1	-
6019	0	0	0	0	1	0	0
6022	1	1	1	0	-	0	-
6023	0	0	0	0	-	0	-
6037	0	0	0	0	-	-	-
6040	0	0	0	0	1	0	0

Appendix A.9. Encounter histories of *Rana clamitans* used in occupancy models by sampling week and site in NJ-DEWA in 2005 (0 = not encountered, 1 = encountered, - = not surveyed).

Site	Primary survey method and sampling week							
	Visual encounter survey			Larval dipnet survey				
	10-Apr	17-Apr	8-May	15-May	12-Jun	19-Jun	10-Jul	17-Jul
122	0	-	0	0	-	-	0	-
232	0	-	0	0	-	-	-	-
271	1	1	1	1	1	1	1	1
302	1	1	1	1	1	1	1	1
367	0	1	1	1	1	1	1	1
429	0	1	1	1	1	1	1	0
435	1	-	1	1	1	1	0	1
494	0	-	0	-	0	-	-	-
517	1	-	1	1	0	1	0	0
569	0	-	0	0	0	0	0	0
625	1	-	1	1	1	-	1	-
667	0	-	0	0	0	0	0	-
668	1	0	1	1	1	1	1	1
684	0	-	0	-	-	-	-	-
694	0	-	0	0	-	-	-	-
758	0	-	0	0	-	-	-	-
787	0	-	0	0	0	-	0	-
816	0	-	0	0	-	-	-	-
818	1	1	1	1	1	1	1	0
870	0	0	0	0	0	0	-	-
905	1	1	1	1	1	0	1	1
963	0	-	0	0	1	-	1	-
968	0	-	0	0	0	1	1	-
1011	1	1	1	1	1	0	1	1
1086	0	-	0	0	-	-	-	-
1096	1	-	1	0	0	1	1	1
2025	0	0	0	-	-	-	-	-
2026	1	1	1	1	1	1	1	1
2031	0	0	0	-	-	-	-	-
2032	0	0	0	0	0	-	-	-
2034	1	-	1	1	1	-	1	-
3010	1	-	1	1	1	-	0	-
3013	0	-	0	0	0	0	0	0
3018	0	-	0	0	0	0	0	0
3019	1	-	0	0	0	-	1	-
3024	0	-	0	-	-	-	-	-
5002	1	0	0	0	0	-	-	-
6001	1	1	0	1	1	1	1	1
6008	1	-	0	0	0	-	1	-
6019	1	0	1	1	1	1	1	1
6022	0	-	0	1	0	-	0	-
6023	1	-	1	1	1	-	1	-
6037	0	0	1	1	0	-	-	-
6040	1	1	1	1	1	1	1	1

Appendix A.10 Encounter histories of *Rana palustris* used in occupancy models by sampling week and site in NJ-DEWA in 2005 (0 = not encountered, 1 = encountered, - = not surveyed).

Site	Primary survey method and sampling week							
	Visual encounter survey			Larval dipnet survey				
	10-Apr	17-Apr	8-May	15-May	12-Jun	19-Jun	10-Jul	17-Jul
122	0	-	0	0	-	-	0	-
232	0	-	0	0	-	-	-	-
271	0	0	0	0	1	1	1	0
302	0	1	1	1	0	0	1	0
367	0	0	0	0	0	0	0	0
429	0	0	0	0	0	0	0	0
435	0	-	0	0	0	0	0	0
494	0	-	0	-	0	-	-	-
517	0	-	0	0	0	0	1	0
569	1	-	0	0	0	0	0	0
625	0	-	0	0	0	-	0	-
667	0	-	0	0	0	0	0	-
668	0	0	0	0	0	0	0	0
684	0	-	0	-	-	-	-	-
694	0	-	0	0	-	-	-	-
758	0	-	0	0	-	-	-	-
787	0	-	0	0	0	-	0	-
816	0	-	0	0	-	-	-	-
818	1	1	0	0	1	1	0	1
870	0	0	0	0	0	0	-	-
905	1	1	0	1	0	0	1	0
963	0	-	0	0	1	-	0	-
968	1	-	0	1	1	1	1	-
1011	1	1	0	1	0	1	1	1
1086	0	-	0	0	-	-	-	-
1096	1	-	1	1	1	0	1	0
2025	0	0	0	-	-	-	-	-
2026	1	1	0	0	0	1	0	0
2031	0	0	0	-	-	-	-	-
2032	0	0	0	0	0	-	-	-
2034	0	-	0	1	1	-	0	-
3010	0	-	0	0	0	-	0	-
3013	0	-	0	0	0	0	0	0
3018	0	-	0	0	0	0	0	0
3019	0	-	0	0	0	-	0	-
3024	0	-	0	-	-	-	-	-
5002	0	0	0	0	0	-	-	-
6001	1	0	0	1	1	1	1	0
6008	0	-	0	1	1	-	1	-
6019	1	0	0	1	0	0	0	0
6022	0	-	0	0	0	-	0	-
6023	1	-	0	0	0	-	0	-
6037	1	1	0	1	1	-	-	-
6040	1	0	0	1	0	0	1	0

Appendix A.11. Encounter histories of *Rana sylvatica* used in occupancy models by sampling week and site in NJ-DEWA in 2005 (0 = not encountered, 1 = encountered, - = not surveyed).

Site	Primary survey method and sampling week						
	Visual encounter survey			Larval dipnet survey			
	10-Apr	17-Apr	8-May	15-May	12-Jun	19-Jun	10-Jul
122	1	-	1	1	-	-	0
232	1	-	1	1	-	-	-
271	1	1	0	1	1	0	0
302	1	1	1	1	1	0	0
367	1	1	1	1	1	0	0
429	1	1	1	1	1	0	0
435	0	-	1	1	1	1	0
494	1	-	1	-	0	-	-
517	0	-	0	0	0	0	0
569	0	-	0	0	0	0	0
625	0	-	0	0	0	-	0
667	0	-	1	1	1	1	1
668	0	0	0	0	0	0	0
684	1	-	0	-	-	-	-
694	1	-	0	1	-	-	-
758	1	-	1	1	-	-	-
787	0	-	0	0	0	-	0
816	1	-	1	1	-	-	-
818	0	0	0	0	0	0	0
870	1	1	0	1	1	0	-
905	0	0	0	0	0	0	0
963	0	-	0	0	0	-	0
968	0	-	0	0	0	0	0
1011	0	0	0	0	0	0	0
1086	1	-	1	1	-	-	-
1096	1	-	0	0	0	0	0
2025	1	1	0	-	-	-	-
2026	0	1	0	1	0	0	0
2031	1	1	1	-	-	-	-
2032	1	1	0	1	1	-	-
2034	1	-	1	1	0	-	0
3010	1	-	0	1	1	-	0
3013	1	-	1	1	1	1	1
3018	0	-	1	1	1	1	0
3019	1	-	1	1	0	-	0
3024	0	-	0	-	-	-	-
5002	1	1	1	1	0	-	-
6001	0	0	0	0	0	0	0
6008	0	-	0	0	0	-	0
6019	0	0	0	0	0	0	0
6022	0	-	0	0	0	-	0
6023	0	-	0	0	0	-	0
6037	1	1	0	1	1	-	-
6040	0	0	0	1	0	0	0

Appendix A.12. Encounter histories of fish used in occupancy models by sampling week and site in NJ-DEWA in 2005 (0 = not encountered, 1 = encountered, - = not surveyed).

Site	Primary survey method and sampling week							
	Visual encounter survey			Larval dipnet survey				
	10-Apr	17-Apr	8-May	15-May	12-Jun	19-Jun	10-Jul	17-Jul
122	0	-	0	0	-	-	0	-
232	0	-	0	0	-	-	-	-
271	0	0	1	1	1	1	0	0
302	0	0	0	0	0	0	0	0
367	0	0	0	0	0	0	0	0
429	0	0	0	0	0	1	0	0
435	0	-	0	0	0	0	0	0
494	0	-	0	-	0	-	-	-
517	1	-	0	0	0	0	0	0
569	1	-	0	0	1	0	0	0
625	1	-	1	0	0	-	0	-
667	0	-	0	0	0	0	0	-
668	0	0	0	0	0	0	0	0
684	0	-	0	-	-	-	-	-
694	0	-	0	0	-	-	-	-
758	0	-	0	0	-	-	-	-
787	0	-	0	1	1	-	0	-
816	0	-	0	0	-	-	-	-
818	1	1	1	1	1	1	1	1
870	0	0	0	0	0	0	-	-
905	0	0	1	0	0	0	1	1
963	0	-	1	1	1	-	1	-
968	1	-	0	1	1	1	1	-
1011	1	0	1	1	1	1	1	1
1086	0	-	0	0	-	-	-	-
1096	1	-	1	1	1	1	1	1
2025	0	0	0	-	-	-	-	-
2026	0	0	0	0	0	0	0	0
2031	0	0	0	-	-	-	-	-
2032	0	0	0	0	0	-	-	-
2034	0	-	0	0	0	-	0	-
3010	0	-	0	0	0	-	0	-
3013	0	-	0	0	0	0	0	0
3018	0	-	0	0	0	0	0	0
3019	0	-	0	0	0	-	0	-
3024	0	-	0	-	-	-	-	-
5002	0	0	0	0	0	-	-	-
6001	1	1	1	0	1	1	1	1
6008	1	-	0	1	1	-	1	-
6019	0	0	0	0	0	0	0	0
6022	1	-	1	1	1	-	1	-
6023	0	-	0	0	0	-	0	-
6037	1	0	1	0	0	-	-	-
6040	1	1	1	1	1	1	1	1

APPENDIX B: DATASHEETS USED

Appendix B.1. Datasheet for amphibian visual encounter surveys performed at sites in NJ-DEWA during 2005.

AMPHIBIAN VES AND DAYTIME CALL SURVEY DATA SHEET
USGS-Leetown Science Center POBS-NJ study 2005

*If found call 814-353-9029 or 304-724-4460

Site _____ Date (m,d,y) _____ Invest _____
 SurveyID# _____ Start Time (24hr) _____ Air Temp(C) _____
 Wind Code _____ Sky Code _____ Noise code _____

CALL AND VISUAL ENCOUNTER SURVEYS

Species Code	Stage*	Time	Abund**	Call/VES	Notes/animal locations

*Life Stage ---(E=egg, L=larvae, A=adult, C=call)
 **Abundance---(1=1-20, 2=21-100, 3= >100, NA=not able to estimate)

Person Minutes: _____ Entire Perimeter (Y/N): _____ Extra Minutes: _____

Time limits (person minutes): <0.1ha=20, 0.15-0.66ha=30, 1-2ha=75, >2ha=90
 *surveys can't be stopped until last 10% of effort uncover no new species

PREDATOR OCCURANCE

	Odonate	Dytiscid	Phyrgan.	Fish centrarch	Fish minnow	Other
Biota (1/0)						

HYDROLOGY

Measurement (cm)	Piezom.	Well-1	Well-2
PVCtop-substrate			
PVCtop-PVCbottom			
PVCtop-H ₂ O outside			
PVCtop-H ₂ O inside			

Drying score

0 = Dry
 1 = 1-10% max
 2 = 10-50% max
 3 = 50-90%max
 4=>90% max

PHOTO INFORMATION

Photo #	Notes	Photo #	Notes

NOTES:

Appendix B.2. Datasheet for amphibian dipnet surveys performed at sites in NJ-DEWA during 2005.

Dipnet Surveys - DEWA Small Wetlands Project

Site: _____ State: _____ Invest: _____

SurveyID: _____ Date : _____ Start Time (24:XX): _____

Individual Sweep Results

Sweep#	Species1, Species2,	Sweep#	Species1, Species2,
1		26	
2		27	
3		28	
4		29	
5		30	
6		31	
7		32	
8		33	
9		34	
10		35	
11		36	
12		37	
13		38	
14		39	
15		40	
16		41	
17		42	
18		43	
19		44	
20		45	
21		46	
22		47	
23		48	
24		49	
25		50	

Sweep#	Species1, Species2,	Sweep#	Species1, Species2,
51		76	
52		77	
53		78	
54		79	
55		80	
56		81	
57		82	
58		83	
59		84	
60		85	
61		86	
62		87	
63		88	
64		89	
65		90	
66		91	
67		92	
68		93	
69		94	
70		95	
71		96	
72		97	
73		98	
74		99	
75		100	

Stopping Rule Employed

*surveys can't be stopped until last 10% of sweeps uncover no new species

	Stopping rule (check one)	Extra sweeps needed (Yes/No)
Entire perimeter swept		
180 sweeper minutes		
100 sweeps performed		

Notes:

Total Sweeper Minutes: _____

Appendix B.3. Datasheet for anuran call surveys performed prior to amphibian dipnet surveys at sites in NJ-DEWA during 2005.

**AMPHIBIAN VES AND DAYTIME CALL SURVEY DATA SHEET
USGS-Leetown Science Center POBS-NJ study 2005**

*If found call 814-353-9029 or 304-724-4460

Site _____ Date (m,d,y) _____ Invest _____
 SurveyID# _____ Start Time (24hr) _____ Air Temp(C) _____
 Wind Code _____ Sky Code _____ Noise code _____

CALL AND VISUAL ENCOUNTER SURVEYS

Species Code	Stage*	Time	Abund**	Call/VES	Notes/animal locations

HYDROLOGY

Measurement (cm)	Piezom.	Well-1	Well-2
PVCtop-substrate			
PVCtop-PVCbottom			
PVCtop-H ₂ O outside			
PVCtop-H ₂ O inside			

Drying score

0 = Dry
 1 = 1-10% max
 2 = 10-50% max
 3 = 50-90% max
 4 =>90% max

NOTES:

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