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Hydroperiod of Wetlands and Reproduction in Wood Frogs (*Rana sylvatica*) and Spotted Salamanders (*Ambystoma maculatum*)

Mary Beth Kolozsvary

HYDROPERIOD OF WETLANDS AND REPRODUCTION IN WOOD FROGS (<u>RANA SYLVATICA</u>) AND SPOTTED SALAMANDERS (<u>AMBYSTOMA MACULATUM</u>)

By

Mary Beth Kolozsvary

B.S. SUNY – College of Environmental Science and Forestry, 1988

M.S. Purdue University, 1998

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Advisory Committee:

Aram J. K. Calhoun, Assistant Professor of Wetland Ecology, Co-Advisor

Malcolm L. Hunter,Jr., Libra Professor of Conservation Biology and Professor of Wildlife Ecology, Co-Advisor

William E. Glanz, Associate Professor of Zoology

Alex Huryn, Associate Professor of Aquatic Entomology

Raymond J. O'Connor, Professor of Wildlife Ecology

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Thesis Co-Advisors: Dr. Aram J. K. Calhoun and Dr. Malcolm L. Hunter, Jr.

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Many amphibians rely on wetlands for reproduction and the differential distribution of amphibian species along a gradient of wetland permanence is striking, yet not absolute. Wood frogs (*Rana sylvatica*) and spotted salamanders (*Ambystoma maculatum*) are thought to rely on seasonal wetlands for greatest breeding success, but there is little documentation of their reliance on these or other habitats. In my first chapter, I studied these species in wetlands across a hydrologic gradient from seasonal wetlands of short flood duration to permanently flooded sites. My results indicate that wood frogs have greatest reproductive effort and success in seasonal wetlands of short flood duration; however, for spotted salamanders, greatest reproductive effort occurs in some permanently flooded wetlands as well as seasonal wetlands of long flood duration.

In chapter 2, I investigated hydrological characteristics and landscape setting of breeding pools for wood frogs and spotted salamanders. High numbers of wood frog egg masses were associated with variables that are all typical of seasonal wetlands that consistently dry in early to mid-summer, whereas high numbers of spotted salamander egg masses were associated with variables that are indicative of more permanently flooded wetlands. I developed a series of decision rules that predict how pool and landscape characteristics constrain breeding population

size in pools for a subset of the sites; I then validated these decision trees with the remainder of the study sites.

In Chapter 3, I evaluated the efficiency at documenting species presence or in capturing individuals for 4 larval sampling techniques. I compared the use of dip nets, pipe samplers, funnel traps, and bottle traps. Funnel traps had the highest probability of detection for a given level of effort (i.e., number of stations) across species. Depending on the species, bottle traps, dip nets, or pipe samplers had the lowest probability of detection per unit effort. Funnel traps or pipe samplers generally captured the highest number of individuals for a given species; dip nets or bottle traps typically yielded the lowest numbers of individuals across species.

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Chapter 1

CONSTRAINTS OF FLOOD DURATION OF WETLANDS ON REPRODUCTION IN WOOD FROGS AND SPOTTED SALAMANDERS

ABSTRACT

Many amphibians rely on wetlands for reproduction and the differential distribution of amphibian species along a gradient of wetland permanence is striking, yet not absolute. In recent years, conservationists have become concerned about declines in populations of wood frogs (*Rana sylvatica*) and spotted salamanders (*Ambystoma maculatum*) over much of their range. These species are thought to rely on seasonal wetlands for greatest breeding success, but there is little documentation of their reliance on these or other habitats. My objective was to determine what pool hydroperiod provides the best conditions for successful reproduction of these species. I documented reproductive effort for wood frogs and spotted salamanders in 72 wetlands in Acadia National Park, Maine in 2000 and 2001. In one or both years, I also examined egg and larval mortality patterns and density of invertebrate predators in a subset of 21 of these wetlands that represent a hydrologic gradient from seasonal wetlands of short flood duration to permanently flooded sites. In 2001, I obtained an index of reproductive success at a subset of 15 of the 21 wetlands. My results indicate that wood frogs have greatest reproductive effort and success in seasonal wetlands of short flood duration; however, for spotted salamanders, greatest reproductive effort occurs in some permanently flooded wetlands as well as seasonal wetlands of long flood duration that have sufficient flood duration to allow development of eggs and larvae in at least some years. Mortality of eggs for wood frogs is generally low across the gradient of flood duration and is higher for spotted salamanders. Larval mortality patterns also differ for the two species: wood frogs have higher mortality in wetlands of long flood duration, whereas spotted salamanders have higher mortality in wetlands of short flood duration. Density of invertebrate predators generally increases with increasing flood duration and larval mortality of wood frogs is significantly correlated with density of invertebrate predators, thus indicating that the vulnerability

of wood frog larvae to predation may limit their ability to successfully reproduce at sites of long flood duration.

INTRODUCTION

Seasonal wetlands typically undergo an annual or longer than annual drying cycle that often supports a specialized biota that can survive the dry phase through some aspect of their life cycle (e.g., seasonal migration, diapause, biphasic life cycle) (Wiggins et al. 1980, Williams 1987, Schwartz and Jenkins 2000). Seasonal wetlands are often referred to as autumnal or vernal pools, depending on whether the basins typically refill with water in the fall or spring (Wiggins et al. 1980). This cyclic drying regime results in a unique suite of species, many of which do not occur or have reduced abundances in permanently flooded wetlands, occupying these seasonal wetlands. Different mechanisms are responsible for determining community structure in wetlands, as it varies across the gradient of flood duration (Wilbur 1987, Schneider and Frost 1996, Wellborn et al. 1996). Faunal communities in seasonal wetlands of short flood duration are typically shaped by the duration of standing water along with competition for food, with predation being a less important force (Wilbur 1987). In wetlands of long to permanent flood duration, predation is typically a more important determinant of community composition, while duration of standing water and competition decrease in importance (Wilbur 1987, Skelly 1996, Skelly 1997).

Seasonal wetlands are often isolated and small in size and, by definition, are ephemeral habitats; thus, they have been traditionally considered of lesser value than larger or more permanent wetlands (Kenney 1995). Consequently, our knowledge of seasonal wetlands is limited because they have been less well-studied than their permanent counterparts (Wiggins et al. 1980, Williams 1987, Schwartz and Jenkins 2000). Furthermore, because of their small size, seasonal wetlands are often unprotected by current wetland regulations (Preisser et al. 2000); hence, they are subject to intense pressure from development in many areas. Because many species rely on these threatened wetlands, there has been an increasing interest in documenting

their value and protecting them from development (Tappan 1997, Gibbs 2000, Preisser et al. 2000, Semlitsch 2000, Snodgrass et al. 2000, Calhoun and Klemens 2002).

In the northeastern United States, some species of invertebrates (e.g., fairy shrimp) and vertebrates (e.g., many amybstomid salamanders) that breed in seasonal wetlands have been used as indicators of seasonal wetlands that are important for maintaining breeding populations of these species (Tappan et al. 1997, Calhoun 2003). Both wood frogs and spotted salamanders typically lay their eggs in these ephemeral wetlands and are thought to rely on them for maximal breeding success (Calhoun 2003); in fact, in some states they have been referred to as obligate breeders in these ephemeral wetlands (Colburn 1997, Tappan et al. 1997). These species are thought to experience higher reproductive success in seasonal wetlands as a result of decreased predation pressure on eggs and larvae and, thus, to survive to metamorphosis better than in permanent pools.

Both wood frogs and spotted salamanders have similar life history characteristics (i.e., early spring breeding, rapid egg and larval development, biphasic aquatic/terrestrial life cycle) which are thought to enable them to exploit seasonal wetlands for breeding (Tyning 1990, Calhoun 2003); however, their reliance on these habitats has not been tested empirically. Furthermore, these two species differ somewhat in these life-history characteristics and are therefore likely to differ in optimal breeding habitats. For example, wood frogs are explosive breeders, whereas spotted salamanders have a more prolonged breeding season; both eggs and larvae develop more rapidly in wood frogs (eggs: 7 – 21 days, larvae: 60 – 70 days) than spotted salamanders (eggs: 30 – 60 days, larvae: 30 – 120 days) (Tyning 1990). Furthermore, the life span of wood frogs is about 4 years (Berven 1990) and of spotted salamanders is 15 – 20 years (Hunter et al. 1999), thus wood frogs therefore have fewer opportunities to breed in their lifetime. I predicted that these differences in life-history characteristics, as well as differential competition and predation pressures on eggs and larvae that varies across the hydrologic gradient, would differentially affect reproductive and survivorship patterns for the 2 species.

To determine relationships between wetland flood duration and reproduction in wood frogs and spotted salamanders, I selected 72 wetlands that represented a hydrologic gradient

from seasonal wetlands of short flood duration to permanently flooded sites. I evaluated 2 measures of reproduction: (1) reproductive effort and (2) reproductive success from egg stage to metamorphosis. I also examined egg and larval mortality patterns and related them to the density of invertebrate predators across this hydrologic gradient. Lastly, to put my findings into a long-term context, I measured date of drying of the seasonal wetlands and compared the amount of precipitation during the study to historic precipitation data. I predicted that wood frogs would have greatest reproductive effort and success in wetlands of short flood duration, and that spotted salamanders would experience greater reproductive effort and success in seasonal wetlands of long flood duration, as a result from reduced predation pressure from fish and invertebrate predators. I also predicted that low rates of egg and larval mortality would generally correspond to that portion of the hydrologic gradient in which the species experiences greatest reproductive effort and success. However, I expected that the influence of egg mortality on the reproductive effort and success of wood frogs would be less important than for spotted salamanders because wood frog egg deposition is earlier and development times are much more rapid. In addition, I expected that wood frog larvae might be more vulnerable to predation than spotted salamander larvae because of trade-offs between the ability to garner resources for rapid growth and development and the ability to avoid predation, as has been indicated in other larval amphibians (Skelly 1996).

METHODS

Study Area

The study area was located along the mid-coast of Maine on the Mount Desert Island (MDI) portion of Acadia National Park, Hancock County (44^0 13' – 44^0 27' North, 68^0 10' – 68^0 26' West). MDI was 280 km^2 of which approximately half (122 km^2) is within Park boundaries. The landscape consisted of north-south oriented ridges separated by deep U-shaped valleys (Patterson et al 1983). The highest elevation (466 m) was on the northeast portion of the island at the summit of Cadillac Mountain. MDI was situated at the southern limit of the spruce-fir

northern hardwoods zone (Westfeld et al. 1956), in the Fundy Coastal and Interior section of the Laurentian Mixed Forest (Bailey 1995; Bailey et al. 1994). Upland soils were dominated by thin, granitic soils (Gilman et al. 1988; Chapman 1970), whereas organic soils were common in wetlands (Calhoun et al. 1994). Six percent of the island contained palustrine wetlands, with most concentrated in the eastern half of the island. Ponds and lakes covered 4% of the island, 25 of which are greater than 3 ha in area.

In 1947, a fire burned 69 km^2 of the northeastern portion of Mount Desert Island. Regeneration of vegetation created an increase in the food supply for beaver (*Castor canadensis*), in particular aspen (*Populus* spp.). In turn, this resulted in a dramatic increase in beaver in the park and the creation of extensive networks of wetlands on the east side of the island. Subsequently, food supply for the beaver and its populations began to decrease and, thus, many of the current wetlands are abandoned beaver flowages.

Study Site Selection

I identified potential study sites from National Wetland Inventory (NWI) maps and smaller wetlands not mapped on NWI that were locally known or that were encountered during preliminary surveys. Wetland study sites were initially selected to represent gradients of four variables: 1) size of wetland (0.01 – 12.00 ha), 2) cover type, 3) hydrogeomorphic setting (i.e., isolated versus connected to a permanent or intermittent stream), and 4) presence or absence of beaver. I sampled breeding amphibians and monitored water level and drying date in 72 wetlands from March through September 2000 and 2001. Twenty-two of the 72 sites had fish present; half these sites were dominated by 2 species of small fish: ninespine sticklebacks (*Pungitius pungitius*) and northern redbelly dace (*Phoxinus eos*). Because most of the 72 sites were considered permanent (29 of 72 = 40%), a subset of 21 sites (0.01 – 1.58 ha in area) that contributed a hydrologic gradient of permanency from seasonal wetlands of short flood duration to permanently flooded wetlands were selected for more intensive sampling. Only 3 of the subset of 21 sites contained fish.

Sampling Methods

Egg Mass Counts. To determine reproductive effort for wood frogs and spotted salamanders (which I used as an index of breeding population size) I counted egg masses in April 2000 and 2001at all 72 wetlands. I considered all flooded areas of the wetlands less than 1 m in depth as potential egg-laying habitat, although in a few sites spotted salamander egg masses were also recorded in areas up to 1.5 m deep. These searches were done at least once each year and the timing was determined based on local site conditions to maximize the number of egg masses detected for both species. Because I returned to the subset of 21 sites frequently, I continued to monitor for any additional egg masses that were deposited and included in those masses in the count.

Egg Mortality and Egg Predator Surveys. In 2001, to determine mortality of eggs, I monitored up to 20 egg masses of each species (range: 2 – 20), beginning as close to day of deposition as possible, at 19 of the 21 sites (due to time constraints). Percent mortality was estimated for each egg mass on each site visit. In addition, I documented whether each egg mass had evidence of predation and I counted the number of predatory caddisflies (Family: Phryganeidae) on each egg mass. I continued to monitor each egg mass from the initial recording until there was evidence of hatching or until the site dried completely, whichever came first. Sites were typically visited bi-weekly and, for a given site, number of mortality estimates for individual egg masses ranged from 1 – 3.

Larval Mortality Surveys. I sampled larval amphibians using pipe samplers on 3 – 4 occasions from mid-May through mid-July, about 2 – 3 weeks apart, from the subset of 21 sites in 2000 and 14 of the 21 sites in 2001 (due to time constraints) (Shaffer et al. 1994). Pipe samplers were constructed from 30 cm diameter culvert pipe, 1 m in height (Skelly 1992). Pipe samples were taken by projecting the pipe sampler roughly 1 m in front of the observer, then pushing it forcibly straight down through the water column. Aquarium dip nets were then used to sample larvae from within the tube. After each scoop, any larvae captured were identified to species and counted. Dip net samples were taken repeatedly, until 5 consecutive sweeps yielded no larval amphibians. Samples were distributed across the pools throughout all areas less than 1 m depth

by placing them along random distances along transects. Number of samples ranged from 5 to 60, based on the approximate area of the site to keep sampling effort in proportion to area.

Metamorph Trapping. I installed linear pitfall traps at 15 of the subset of 21 sites to capture wood frog and spotted salamander metamorphs in 2001, based on the design used by DiMauro (1998). Only 15 sites were trapped due to time constraints; these sites were selected to represent the entire hydrologic gradient. The traps were constructed from black plastic corrugated pipe (10.2 cm diameter x 50 cm length) with a 6 cm wide lengthwise opening cut in the top. The ends of the traps were closed with the bottom of a 350 ml plastic deli container. Traps were installed underground with the opening at ground level. The length-wise openings of the traps were installed parallel to the wetland boundary and were spaced at approximately 2.5 m intervals to cover approximately 20% of the total perimeter of the wetland.

Traps were checked every 2 to 3 days from mid-June through September 2002. Once a site dried completely, I continued to check traps until there had been at least 1 substantial rainfall event that would have triggered movement of metamorphs away from the site and, after that rainfall event, I had 3 consecutive trap checks with no captures. I recorded length (total length for anurans and both total length and snout-vent length for salamander metamorphs) and body mass for metamorphs captured.

Aquatic Predator Sampling. In 2000, I sampled invertebrate predators using pipe samplers from mid-May through mid-August while simultaneously sampling for amphibian larvae (as well as 2 additional sampling periods) from the subset of 21 sites (See larval mortality survey section). Invertebrates were collected from the first 5 scoops of a subset of the pipe samples that were taken during each sampling period (5 – 20, based on the rank area of the site). All invertebrates sampled were identified to family level in the laboratory, except for leeches, which were identified to class. A subset of invertebrates that were in predatory families was also counted; specifically, Orders: Coleoptera, Hemiptera, Odonata and Class: Hirudinea.

Hydroperiod Monitoring. Permanent staff gauges constructed of rebar and PVC pipe, marked at 5 cm intervals, were installed in April 2000. Water levels were recorded at least monthly at all 72 sites from April through August 2000 and 2001. For seasonal wetlands, sites

were checked more frequently when the site was close to drying, to determine actual date of drying. Water levels for the subset of 21 wetlands were also checked more frequently (at least weekly) in both years. All sites that were close to drying by the end of August of 2000 and 2001 were also monitored through October to determine if they subsequently dried.

Precipitation. Daily precipitation data for 1982 – 2001 were obtained from a permanent weather station operated by the National Park Service at Acadia National Park located at McFarland Hill, Hancock County, Maine (44^0 22' 26" North, 68^0 15' 38" West, 129 m). Although other variables (e.g., winter precipitation, groundwater levels, daily temperature) can also affect drying date of seasonal wetlands, I focused on precipitation from 1 April through 31 July because it is likely the most important determinant of actual drying date for these sites. I examined precipitation for the previous 20 years to compare the precipitation amounts during this study with long-term patterns.

Data Analysis

Metrics. Because area of wetland was correlated with flood duration in both years (2000: $r_s = 0.52$, $p < 0.01$; 2001: $r_s = 0.58$, $p < 0.01$) (i.e., small wetlands tended to dry sooner than larger wetlands), I measured reproductive effort as the number of egg masses per m^2 surface area of water less than 1.5 m depth to eliminate potential confounding effects of area. For each site visit, I averaged the estimates of egg mass mortality across all egg masses monitored at a given site and converted it into a proportion, between 0 and 1. To obtain an index of egg mass mortality for each site (range: 0 – 1), I averaged these mean mortality estimates across all site visits for each species (range: 1 – 3 visits for each species for each site). To obtain larval mortality rate estimates for each species for each site, I first estimated larval population size for each species (i.e., number per m^2 surface area of wetland) for 2 – 3 larval sampling periods in both years. Larval sampling periods were only used in calculating larval mortality rates for a given species if I determined that all larvae had hatched from eggs and dispersed from the immediate vicinity of the eggs and none of the larvae had apparently reached metamorphosis. I then calculated larval mortality rates for each species for each of the sites by estimating the slope of a regression of the

natural logs of the population estimates for each of the applicable larval sampling periods over the calendar days the larval sample was taken. To measure reproductive success, I used an index that was parameterized as the number of metamorphs captured per egg mass deposited. To estimate the density of invertebrate predators at each site, I first calculated the number of invertebrate predators per m^2 of surface area sampled for each site for all sample periods in which the site contained water (range: 2 – 6). I then averaged all the density estimates for predatory invertebrates for each site to obtain an overall estimate of the density of invertebrate predators for each of the sites across the sampling period. Flood duration was the length of time a wetland contained water during a given year and was measured as the calendar day that a particular wetland dried. For example, if a wetland dried on 18 July in 2000 and 1 July in 2001, flood duration for that site was 200 for 2000 and 182 for 2001; "365" was used for wetlands that did not dry.

Analysis. I used Spearman's rank correlation to determine if there was a relationship between flood duration of wetlands and both reproductive effort and success for wood frogs and spotted salamanders in 2000 and 2001. I used scatterplots and Spearman's rank correlation to examine patterns of egg and larval mortality for both wood frogs and spotted salamanders across the gradient of flood duration of wetlands. I examined correlations between egg mass mortality and both the proportion of egg masses that had evidence of predation and the mean number of predatory caddisflies counted per egg mass. I also examined correlations between larval mortality and the density of invertebrate predators. I used scatterplots to examine overall patterns of predation on egg masses and the density of invertebrate predators across the gradient of flood duration of wetlands.

RESULTS

Reproductive Effort

Wood frog egg masses were documented in approximately half of the 72 study sites (37 in 2000 and 39 in 2001); maximum number of egg masses counted at a site in a given year was

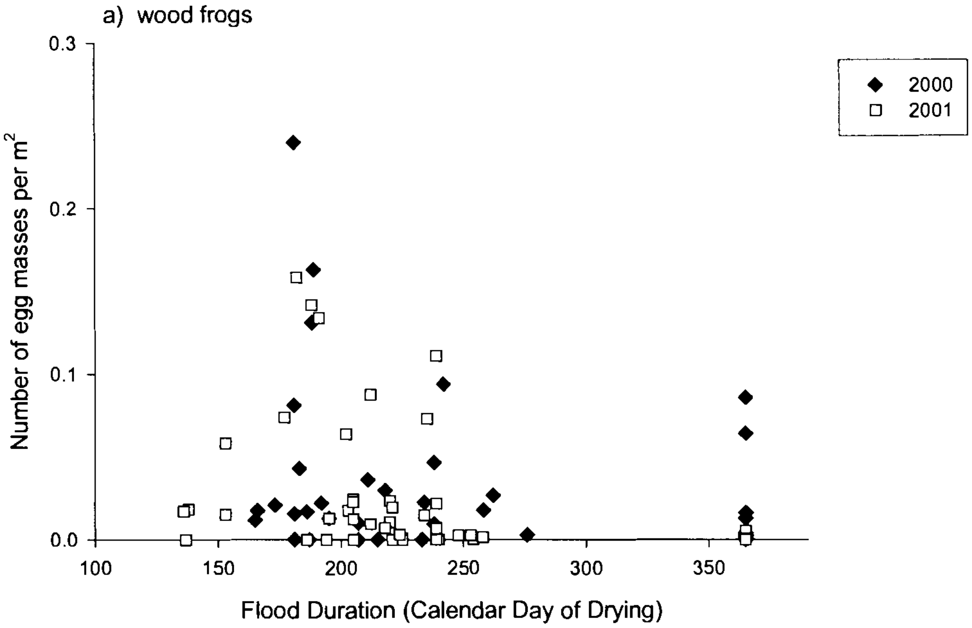
153. In contrast, spotted salamanders bred at nearly all the 72 sites (69 in both 2000 and 2001); maximum number of egg masses counted at a site in a given year was 913. Reproductive effort of both species was greater in wetlands of short flood duration in both years (wood frogs: 2000: $r_s = -0.56$, $p < 0.01$, 2001: $r_s = -0.61$, $p < 0.01$; spotted salamanders: 2000: $r_s = -0.35$, $p < 0.01$, 2001: $r_s = -0.31$, $p = 0.01$) (Figure 1.1). Numbers of egg masses for both wood frogs ($r_s = 0.90$, $p<0.01$) and spotted salamanders ($r_s = 0.80$, $p<0.01$) was similar between years across all sites.

Egg and Larval Mortality

Egg mortality was relatively low for wood frogs across the gradient of flood duration and it was higher for spotted salamanders than for wood frogs, especially at intermediate flood durations (range of the index of egg mortality was: 0.00 – 0.31 for wood frogs; 0.00 – 0.74 for spotted salamanders) (Figures 1.2a and 1.2b). Larval mortality rates for wood frogs ranged from 0.008 – 0.876 and increased with flood duration of wetland (Figure 1.2c). In contrast, larval mortality rates of spotted salamanders ranged from 0.006 – 1.091 and decreased with flood duration of wetland (Figure 1.2d).

Reproductive Success

A total of 377 wood frog metamorphs were captured between 23 June and 4 August 2001 at 10 of the 15 sites. In contrast, only 10 spotted salamander metamorphs were captured between 28 July and 27 September 2001 at 4 of the 15 sites. One site dried prior to mid-June, well before any of the wood frog tadpoles could have reached metamorphosis and before any spotted salamander egg masses had hatched. The earliest evidence of spotted salamanders reaching metamorphosis was from a capture on 6 August from a site that had dried on 21 July. Apparently, movement from the site had been delayed until a precipitation event that was significant enough to trigger initial emigration. Reproductive success in wood frogs was generally greater in wetlands of short or intermediate flood durations ($r_s = -0.59$, $p < 0.05$) (Figure 1.3a), but wetland duration was not related to reproductive success in spotted salamander ($r_s = 0.35$, $p = 0.20$) (Figure 1.3b). Despite the lack of a linear relationship between flood duration and



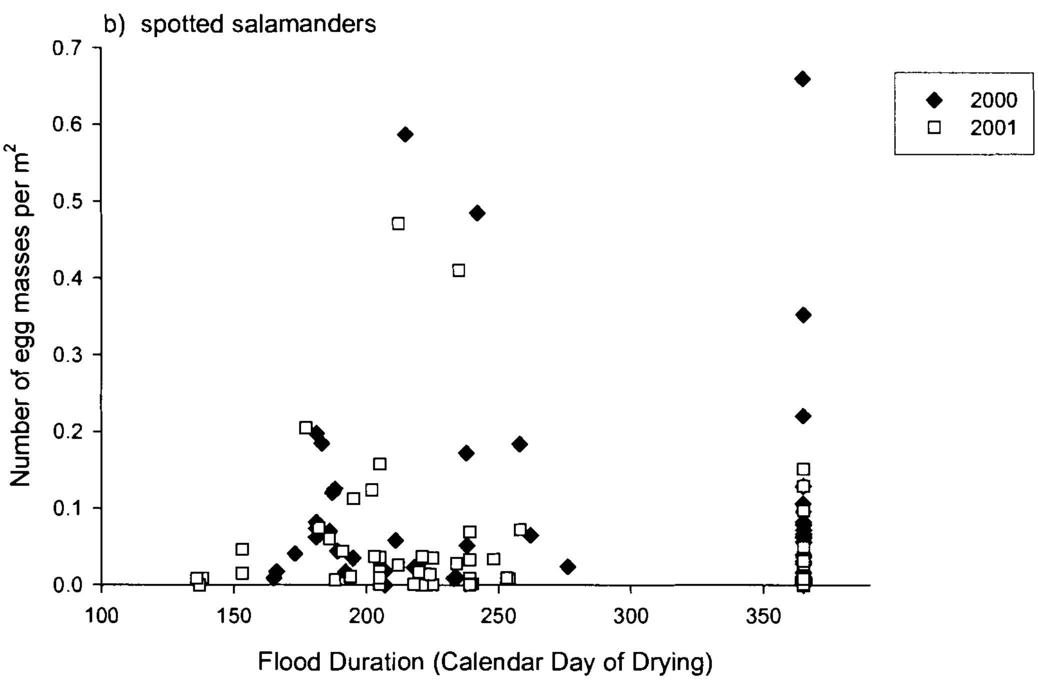
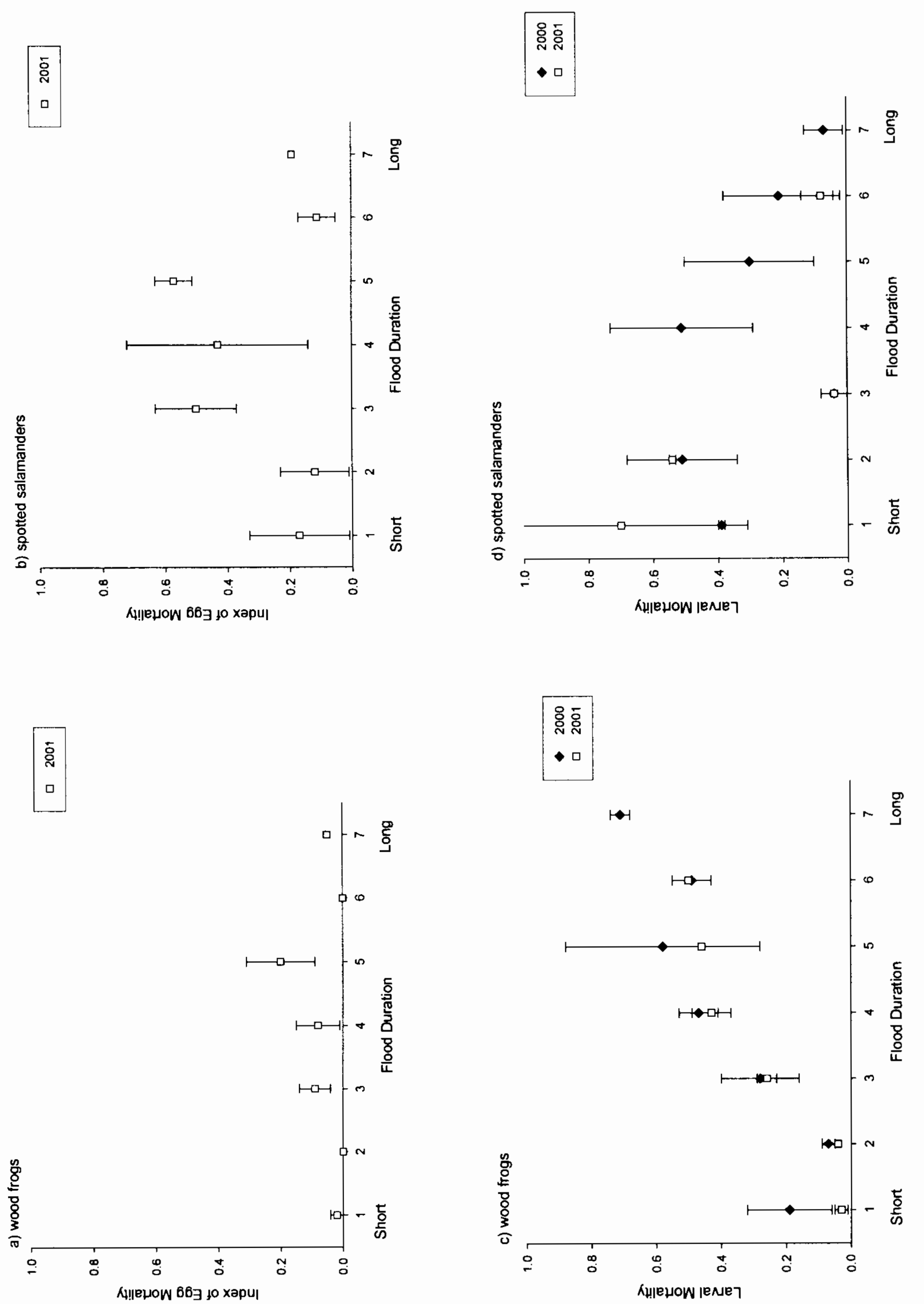


Figure 1.1. Number of egg masses per m^2 surface area of water for a) wood frogs and b) spotted salamanders in relation to flood duration for 72 wetlands in Acadia National Park, Maine in 2000 and 2001 (Flood duration of wetlands that contained water through 31 December = 365).


a) wood frogs
Index of Egg Mortality
1.0
0.8
0.6
0.4
0.2
0.0
1
2
3
4
5
6
7
Short
Flood Duration
Long
2001
b) spotted salamanders
Index of Egg Mortality
1.0
0.8
0.6
0.4
0.2
0.0
1
2
3
4
5
6
7
Short
Flood Duration
Long
2001
c) wood frogs
Larval Mortality
1.0
0.8
0.6
0.4
0.2
0.0
1
2
3
4
5
6
7
Short
Flood Duration
Long
2000
2001
d) spotted salamanders
Larval Mortality
1.0
0.8
0.6
0.4
0.2
0.0
1
2
3
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7
Short
Flood Duration
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2000
2001

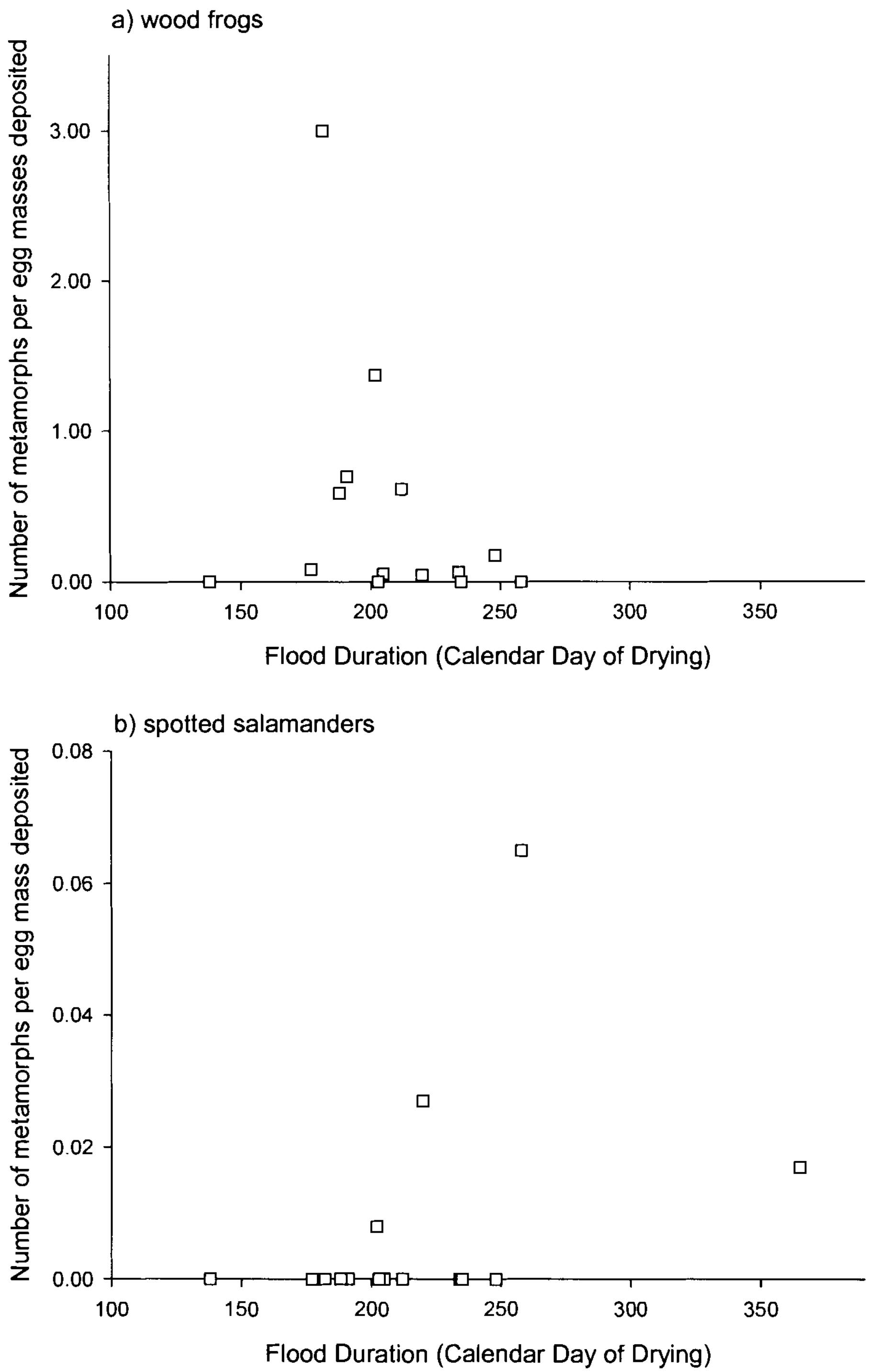

Figure 1.3. Number of metamorphs captured in pitfall traps per egg mass deposited for a) wood frogs and b) spotted salamanders in relation to flood duration for 15 wetlands in Acadia National Park, Maine in 2001.

reproductive success in spotted salamanders, no metamorphs were captured at the 6 of 21 sites that dried prior to 21 July.

Aquatic Predators of Amphibian Eggs and Larvae

The proportions of wood frog and spotted salamander egg masses that were predated were significantly correlated with the indices of egg mortality (wood frog: $r_s = 0.54$, $p < 0.03$; spotted salamander: $r_s = 0.69$, $p < 0.01$). The indices of egg mortality for both amphibian species were also significantly correlated with the mean number of predatory caddisflies per egg mass (wood frog: $r_s = 0.56$, $p = 0.02$; spotted salamander: $r_s = 0.79$, $p < 0.01$) (Figure 1.4). The mortality of wood frog larvae increased with increasing density of invertebrate predators (Figure 1.5a), but no pattern was apparent between the mortality of spotted salamanders and density of invertebrate predators (Figure 1.5b) (wood frog: $r_s = 0.54$, $p < 0.03$; spotted salamander: $r_s = -0.21$, $p > 0.20$). Mean number of predatory caddisflies per egg mass was highest in seasonal wetlands of long duration and semi-permanently flooded sites (Figure 1.6a), whereas the density of invertebrate predators ranged from 0.80 – 4.37 per m^2 of surface area sampled and increased with increasing flood duration of wetlands (Figure 1.6b).

Precipitation and Flood Duration

Precipitation during the focal period (1 April through 31 July) was 481 mm in 2000 and 212 mm in 2001. Over the last 20 years the range of precipitation during the focal period was from 171 to 602 mm. In comparison to the past 20 years, 2000 was moderately wet (rank: 5 of 20; rank 1 is the year of greatest precipitation) and 2001 was very dry (rank: 18 of 20). Of the 72 total sites, 28 dried in 2000 and 42 dried in 2001 (Figure 1.7). Furthermore, of the 15 sites that were trapped for metamorphs, 11 in 2000 and 14 dried in 2001. Of these 15 sites, only one site dried prior to wood frogs reaching metamorphosis, whereas 6 sites dried before spotted salamanders reached metamorphosis. Although there was a >250 mm difference in the amount of precipitation during the focal period between 2000 and 2001, date of drying for seasonal wetlands did not differ greatly between years.

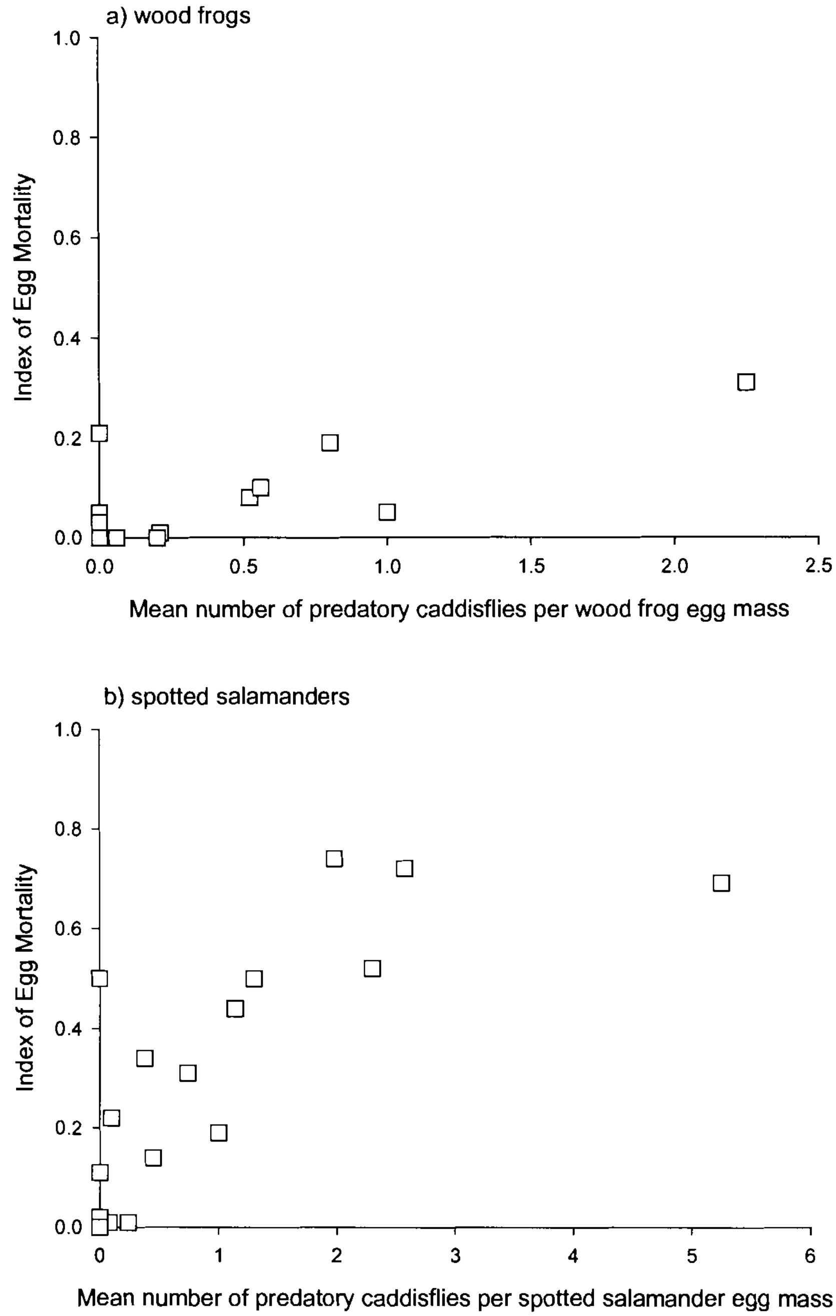

Figure 1.4. Index of egg mortality for a) wood frogs and b) spotted salamanders in relation to the mean number of predatory caddisflies (Family: Phryganeidae) observed on egg masses per total number of egg masses monitored for 21 wetlands in Acadia National Park, Maine in 2001.

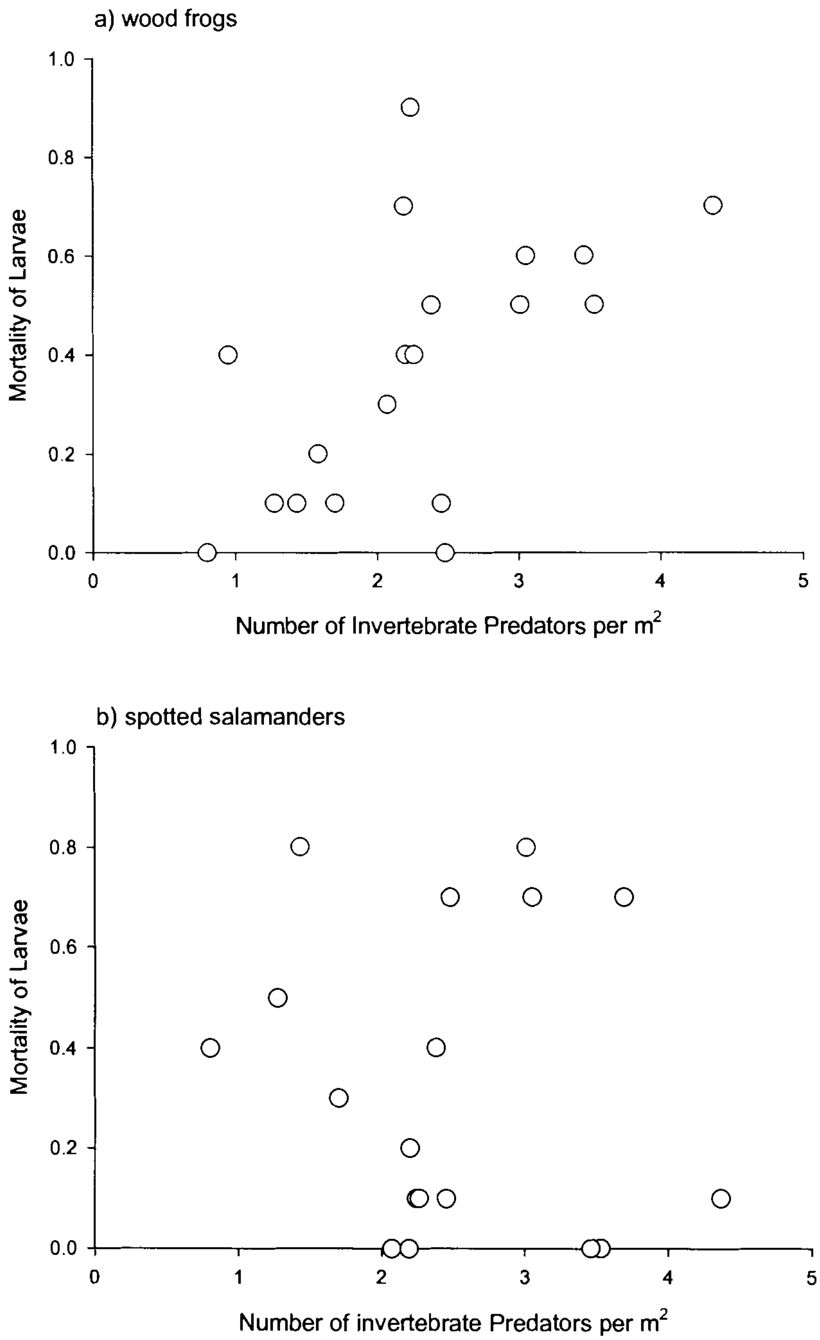

Figure 1.5. Mean larval mortality of a) wood frogs and b) spotted salamanders in relation to density of invertebrate predators (number per m^2 of surface area sampled) for 21 wetlands in Acadia National Park, Maine in 2000 and 2001.

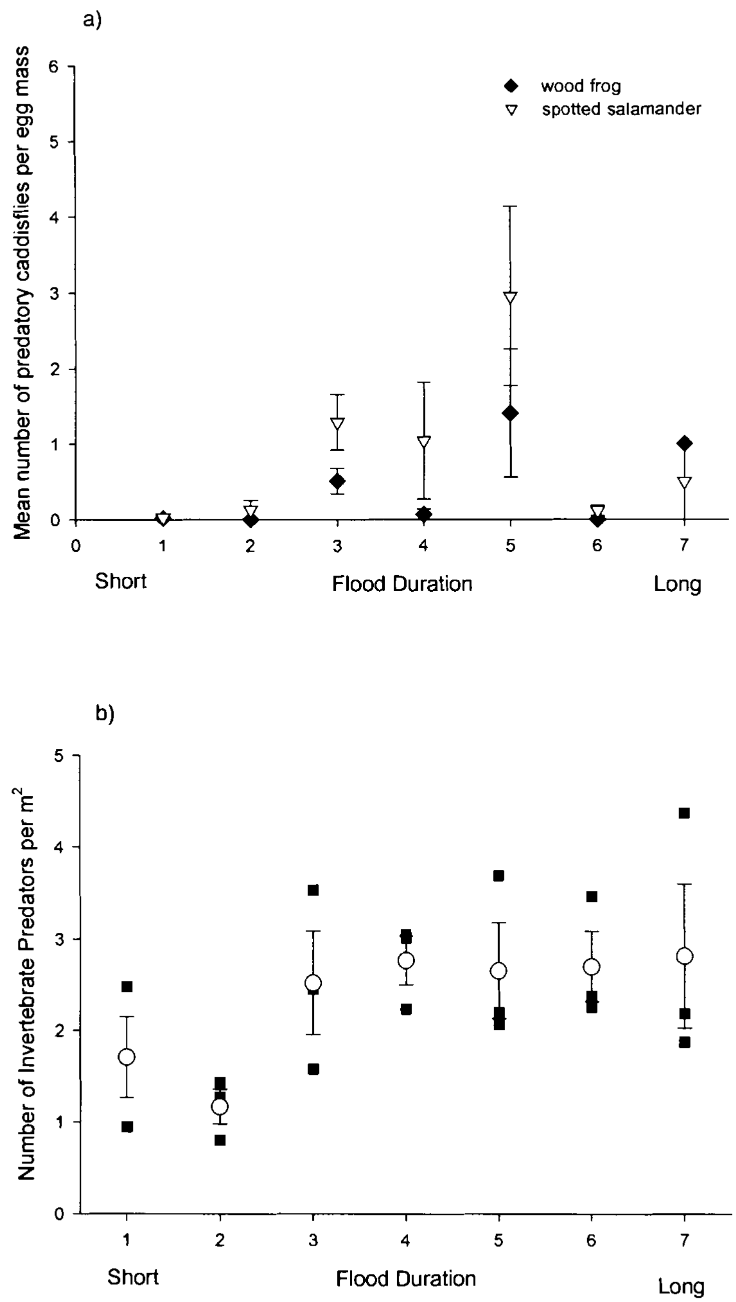

Figure 1.6. Categories of flood duration for 21 wetlands in Acadia National Park, Maine in relation to a) mean number of predatory caddisflies (Family: Phryganeidae) observed on egg masses monitored in 2001 and b) density of invertebrate predators (Orders: Coleoptera, Hemiptera, Odonata, and Class: Hirudinea) (number per m^2 of surface area sampled) in 2000.

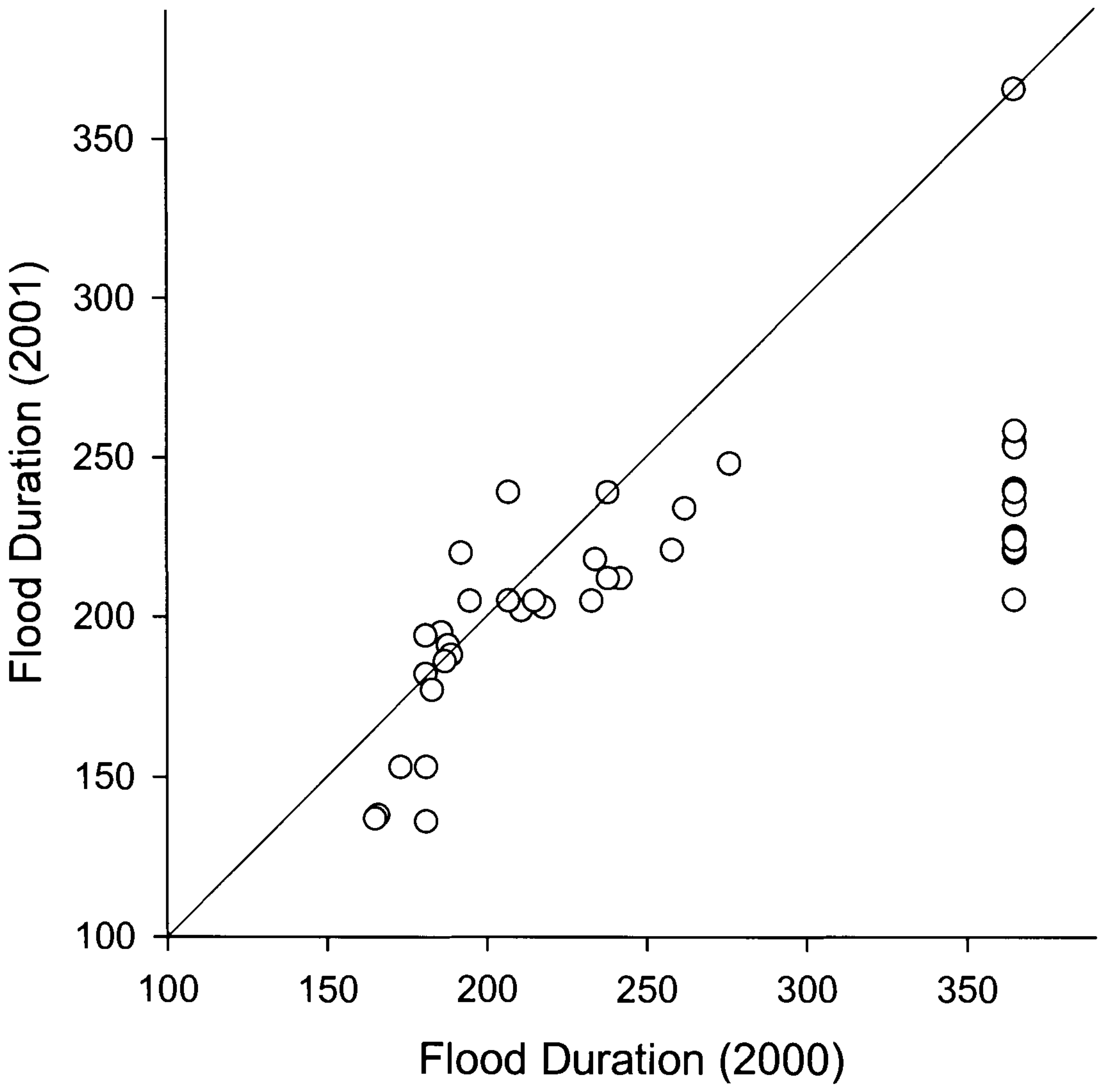

Figure 1.7. Flood duration of 72 wetlands in Acadia National Park, Maine in 2000 versus 2001.

DISCUSSION

Reproductive Effort and Success

Reproductive effort and success of wood frogs was greatest in seasonal wetlands of short flood duration. This is consistent with other amphibians (e.g., chorus frogs, *Pseudacris triseriata*) that breed early in the season in temporary pools and have rapid egg and larval development times (Skelly 1995). Figures 1.1a and 1.3a illustrate these relationships for wood frogs and also highlight the variability of these attributes among sites with similar flood duration. This variability emphasizes that flood duration is not the sole predictor of reproductive effort or success for wood frogs, but rather acts as a primary organizing or constraining variable that serves to limit the maximal breeding population size and reproductive success of wood frogs across this gradient. These results are consistent with other studies and current hypotheses (Skelly 1996, Wellborn et al. 1996, Skelly 1997). Sites on the short flood duration end of the gradient will have a greater likelihood of drying prior to wood frog larvae reaching metamorphosis in a given year than sites that typically have longer flood duration; this may limit recruitment in that year. Because wood frog metamorphs exhibit high natal philopatry and adults exhibit high breeding-site fidelity (Berven and Grudzien 1990), future breeding population size at a given site will be affected by low recruitment (Berven 1990).

Sites with long flood duration also appear to limit the maximal breeding population size at a given site, probably because of biotic factors (e.g., predation, competition) (Figures 1.4, 1.5, and 1.6) (Wilbur 1987, Skelly 1996, Skelly 1997). These effects may serve to depress breeding population size, but with a less pronounced effect than sites with a high risk of drying prior to metamorphosis (Figure 1.1). This appears reasonable, in that if a site regularly dries prior to metamorphosis, then no recruitment will occur in those years and it will be unlikely to sustain a breeding population. However, if a site contains water for sufficient duration for metamorphosis to occur in all years, yet has high predator populations present, at least some larvae may be able to metamorphose on a regular basis and a breeding population could persist, albeit at low

population size. Recent studies and reviews stress the importance of predation as a strong pressure that shapes faunal communities of longer flood duration (Wellborn et al. 1996, Skelly 1997); my findings for wood frogs support this conclusion. There is evidence that wood frogs are able to detect and avoid breeding in experimental pools that contain predatory fish (Hopey and Petranka 1994); this may extend to an ability to detect pools that contain high populations of invertebrate predators as well, although to my knowledge this has not been investigated in adult wood frogs. Feedback mechanisms that encourage breeding at specific sites that have been productive in the past (e.g., high natal philopatry, high breeding-site fidelity, explosive breeding strategy) may serve to reinforce their breeding distribution. In my study, wood frogs were restricted to approximately half of the 72 study sites; these feedback mechanisms likely contribute to this limited distribution.

Reproductive effort for spotted salamanders had a similar distribution across the hydrologic gradient to that of wood frogs (Figure 1.1b), except that maximal breeding success was documented in seasonal wetlands of relatively long flood duration and some permanently flooded wetlands. This is reasonable in that spotted salamanders have longer egg and larval development times than wood frogs and, are therefore unable to successfully exploit seasonal wetlands of short flood duration. Reproductive success did not indicate a clear pattern across the gradient of flood duration (Figure 1.3b); however, spotted salamander metamorphs were captured only at sites that contained water through mid-July. Based on my knowledge of the typical breeding phenology and emergence of spotted salamanders metamorphs in this area, mid-July would likely be the earliest that spotted salamander larvae would reach metamorphosis in a given year; this is consistent with Windmiller's (1996) findings in eastern Massachusetts. As in Windmiller's study (1996), the majority of spotted salamander metamorphs I captured were in mid- to late August; thus, for seasonal wetlands to serve as habitat for source populations they would have to retain water into August in at least some, if not most, years. Based on long-term precipitation data, it would be unlikely that the sites that are of the shortest flood duration would ever retain water long enough to successfully produce metamorphs (Figure 1.7). There is evidence that spotted salamanders do not select breeding pools based on the probability of

successfully producing young and that this species can maintain breeding populations at reproductive sinks (Ireland 1989), likely as a result of dispersing individuals from neighboring source populations. Accordingly, my findings support the idea that greatest reproductive success occurs in wetlands that, at least in some years, are of long flood duration.

Egg Mortality

As predicted, egg mortality for wood frogs was generally low across the gradient of wetland flood duration, likely a result of their short development time (Figure 1.2). Seigel (1983) also found high survivorship of wood frog egg masses (96.6%) in a 1 year study of a temporary pond in New Jersey. Egg mortality was generally higher for spotted salamanders, with greatest mortality in seasonal wetlands of long flood duration and semi-permanently flooded wetlands. This coincided with those sites that had large numbers of caddisflies (Family: Phryganeidae, Genera: *Ptilostomis*, *Banksiola*) which I observed predating egg masses of both wood frogs and especially spotted salamanders. This is consistent with other studies that have documented large numbers of predatory caddisflies consuming amphibian eggs (Stout and Stout 1992, Rowe et al. 1994).

Larval Mortality

Larval mortality for wood frogs and spotted salamanders differed across the gradient of wetland flood duration (Figure 1.2). As predicted, larval mortality for wood frogs was lowest in wetlands of short flood duration. Researchers have argued that certain species of larval amphibians that are able to successfully exploit wetlands of short flood duration (where the risk of drying before they reach metamorphosis is great) possess behavioral characteristics that enable them to garner resources (e.g., active foraging); however, these same behavioral characteristics may make them more susceptible to predation (Woodward 1983, Skelly 1996). Wood frogs appear to fit this argument, with larval mortality steadily increasing with both increasing flood duration of wetland (Figure 1.2) and density of invertebrate predators (Figure 1.5). In contrast, larval mortality of spotted salamanders decreased with increasing flood duration of wetland (Figure 1.2). High larval mortality in wetlands of short flood duration is expected if these sites dry prior to larvae reaching metamorphosis. Researchers have argued that spotted salamander

larvae may be susceptible to fish predation and, thus have low mortality in seasonal, fish-free wetlands and higher mortality in permanently flooded wetlands (Calhoun 2003). Susceptibility of ambystomid larvae in general has been well demonstrated (Petranka 1983, Tyler et al. 1998a, Tyler et al. 1998b). Because the permanently flooded sites were either fish-free or dominated by small fish that are unlikely to prey on larval amphibians, I cannot address whether spotted salamander larvae experience higher mortality in permanent waters that contain predatory fish (e.g., *Lepomis* spp., *Oncorhynchus* sp., *Salvelinus* sp.). However, my results do indicate that in the absence of larger predatory fish, the risk of a seasonal wetland drying prior metamorphosis appears to have a greater effect on mortality than the influence of high densities of predatory invertebrates (Figure 1.5). Overall, the patterns of mortality of spotted salamander larvae are consistent with my predictions, in that lowest mortality occurs in wetlands of long flood duration (Figure 1.2).

Reproductive Sinks

Reproductive effort for spotted salamanders was not as low in seasonal wetlands of short flood duration as I expected; these wetlands used by spotted salamanders even include sites that likely never retain water long enough to produce metamorphs. Why do spotted salamanders breed at sites that are unlikely to ever produce metamorphs? Given that the risk of a seasonal wetland drying prior to metamorphosis is variable between years (Figure 1.7), dispersing metamorphs of spotted salamanders may not have the ability to distinguish wetlands of short versus long flood duration. Ireland (1989) suggested that spotted salamanders do not select breeding sites based on the probability of successfully producing metamorphs. Perhaps water depth is the only characteristic that a dispersing spotted salamander may use to select a breeding site. Perhaps spotted salamanders that breed in a seasonal wetland produce an abundance of metamorphs only 1 in 5 years, but this may equal the production of spotted salamanders that breed in a permanent, fish-free wetland and produce fewer metamorphs each year. In other words, reproductive longevity would enable spotted salamanders to maintain populations in wetlands of short flood duration with only occasional years of successful reproduction, and these sites may not be reproductive sinks. This has been suggested for pool-breeding amphibians in

several studies, particularly in the southeastern United States (Pechman et al. 1989, Semlitsch et al. 1996, Semlitsch 2002). Spotted salamanders are thought to live up to 20 years, begin reproducing at 2-3 years of age, and breed every other year (Hunter et al. 1999). Dispersal strategy, reproductive longevity, coupled with the lack of feedback mechanisms (i.e., choruses do not attract individuals to breeding sites, they have a prolonged, not explosive, breeding seasons), probably contribute to the maintenance of breeding by spotted salamanders at reproductive sinks.

Summary

In summary, the 2 species show differential adaptations to flood duration of wetlands and its selective pressures. Wood frogs are adapted to wetlands of short flood duration; they probably are good competitors (c.f., other species of tadpoles) for food, but at the cost of their poor ability to escape predation in predator-rich permanently flooded wetlands. Spotted salamanders require wetlands of longer flood duration to reproduce successfully and, may therefore possess behavioral characteristics (e.g., foraging strategies) that enable them to survive in wetlands of long flood duration, even if they have high densities of invertebrate predators. Differences in life span, reproductive longevity, dispersal strategy, and feedback mechanisms during the breeding season may allow spotted salamanders to maintain populations, in which some breed in reproductive sinks.

IMPLICATIONS

This study supports the notion that monitoring numbers of egg masses of wood frogs over time will give an indication of the importance of a particular site for maintaining wood frog populations. Previous studies have shown a relationship between numbers of breeding wood frogs and egg mass numbers (Crouch and Paton 2000). My study supports the link between egg mass numbers and actual site productivity for wood frogs. In contrast, my results indicate that monitoring egg masses of spotted salamanders may be very misleading. In landscapes that are highly permeable to dispersing juveniles, some sites that have consistently high numbers of egg masses of spotted salamanders may actually be sink populations that are being maintained by

dispersing individuals. In other words, high egg mass numbers for spotted salamanders either reflect productivity of the site, productivity of nearby sites, or a combination of both. Furthermore, it is apparent that wood frogs and spotted salamanders do differ in which wetlands are most productive for each species, even though they often breed at the same sites. It appears that wetlands of short flood duration are more important for wood frogs whereas seasonal wetlands of long flood duration and semi-permanently flooded wetlands (if fishless or lacking predatory fish) are more important for spotted salamanders.

Hydroperiod of wetlands is a primary source of variation in amphibian community structure in wetlands and metamorph production of many pool-breeding amphibian species is often episodic, with substantial recruitment into the population occurring only in occasional years (Semlitsch et al. 1996, Semlitsch 2002). Small, isolated wetlands are often unprotected because of their small size but these sites can provide breeding opportunities for amphibians that are able to successfully exploit wetlands of short flood duration, as my study demonstrates for wood frogs and Skelly (1996) has shown for chorus frogs. Other species, such as spotted salamanders, are most successful breeding in wetlands of longer flood duration than for wood frogs, thus my study supports the current consensus that conservationists or managers should focus conservation of pool-breeding amphibians on a landscape approach and treat groups of ponds instead of individual ponds as a conservation unit (Marsh and Trenham 2001, Semlitsch 2002, Snodgrass et al. 2002). Seasonal wetlands provide varying opportunities for metamorph production in pool-breeding amphibians that is largely dependent on weather conditions in a given year (Semlitsch et al. 1996, Babbit et al. 2000), thus a "groups of ponds" approach to conservation of these assemblages will potentially provide successful production of metamorphs for the various species, at least somewhere in the group of ponds in a given year.

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Chapter 2

HYDROLOGICAL CHARACTERISTICS AND LANDSCAPE SETTING OF BREEDING POOLS FOR WOOD FROGS AND SPOTTED SALAMANDERS

ABSTRACT

Hydroperiod has a strong influence on the faunal composition of wetlands. Wood frogs (*Rana sylvatica*) and spotted salamanders (*Ambystoma maculatum*) are thought to rely on seasonal wetlands (vernal pools) for optimal breeding success, but there is little documentation of their reliance on these habitats. My objective was to identify which pool and landscape characteristics are associated with high numbers of breeding individuals. I documented reproductive effort for wood frogs and spotted salamanders by counting egg masses in 72 wetlands in Acadia National Park in 2000 and 2001. For a subset of 21 wetlands, I separated the sites into 3 categories of relative importance based on reproductive effort, for each of the species. High numbers of wood frog egg masses were associated with 4 pool but no landscape variables ($P < 0.05$) that are all typical of seasonal wetlands that consistently dry in early to mid-summer. Significant pool variables that correlated positively with high numbers of wood frog egg masses include: low primary productivity, absence of an inlet, absence of an outlet, and absence of unfrozen water in winter. In contrast, high numbers of spotted salamander egg masses were associated with 4 pool and no landscape variables that are indicative of more permanently flooded wetlands ($P < 0.05$); specifically, high numbers of spotted salamander egg masses were associated with presence of an inlet, presence of an outlet, presence of unfrozen water in winter, and longer categories of flood duration. I developed a series of decision rules to predict relative egg mass numbers in breeding pools for a subset of the sites ($n = 21$) based on pool and landscape characteristics; I then validated and evaluated these decision trees using the remainder of the study sites ($n = 51$). Lastly, my results show that although wood frogs and spotted salamanders often breed in the same sites (3 of the 21 sites were classified as having

high relative importance for both species), the relative order of importance of sites for the 2 species differs.

INTRODUCTION

Wetland hydroperiod, or seasonal fluctuations in water level and drying patterns, is an important determinant of floral and faunal communities (Williams 1987, Mitsch and Gosselink 2000). Many pool and landscape characteristics, including surficial geology (surface area of the pool, basin shape and substrate), hydrogeomorphic setting (hydrologic budgets, slope position, aspect, catchment area and composition), and climate (especially, seasonal precipitation and temperature patterns), can influence wetland hydroperiod (Mitsch and Gosselink 2000).

Species that breed in wetlands generally occur in a subset of wetlands that have suitable hydroperiods. The structure of faunal communities varies along the gradient of wetland hydroperiod in response to multiple mechanisms (Wilbur 1987, Schneider and Frost 1996, Wellborn et al. 1996). For example, communities in wetlands of short flood duration are typically limited by the risk of drying and competition among species, with predation a less important force; in wetlands of long flood duration, predation has a greater influence on community composition, with risk of drying and competition less important (Wilbur 1987, Skelly 1996, Skelly 1997).

Wood frogs (*Rana sylvatica*) and spotted salamanders (*Ambystoma maculatum*) are thought to rely on seasonal wetlands for breeding, but their reliance on them is not absolute, in that they also can successfully breed in permanently flooded wetlands, which lack fish that prey on larval amphibians (Tyning 1990, Hunter et al. 1999). Both wood frogs and spotted salamanders breed in the early spring and have rapid egg and larval development. Development times for wood frog eggs and larvae are more rapid than for spotted salamanders (Hunter et al. 1999) and wood frogs can metamorphose 4 – 12 weeks earlier than spotted salamanders in a given year (Kolozsvary unpublished data). Because the length of egg and larval periods differ for wood frogs and spotted salamanders, wetland hydroperiods that provide ideal breeding sites for the 2 species likely differ.

The purpose of this study was to determine which landscape setting and physical pool characteristics are indicators of the relative importance of breeding sites for these species. I examined reproductive effort of wood frogs and spotted salamanders in 72 wetlands in 2000 and 2001 that represent a gradient of hydroperiod from wetlands of short flood duration to permanently flooded sites. I examined correlations and scatterplots to determine potential relationships between reproductive effort and breeding pool and surrounding landscape characteristics for a subset of these wetlands (n = 21). I then developed and evaluated a series of decision rules to predict relative egg mass numbers of breeding pools for the subset of wetlands based on pool and landscape characteristics. I validated and further evaluated these decision trees using the remainder of the study sites (n = 51) to determine what pool and landscape characteristics are important drivers of reproductive effort for wood frogs and spotted salamanders. I predicted that pool and landscape variables that are associated with wetlands of short flood duration would be correlated with high numbers of wood frog egg masses. In contrast, for spotted salamanders, I predicted that characteristics that are associated with wetlands of longer flood duration would be correlated with high numbers of egg masses.

METHODS

Study Area

I studied these species on the Mount Desert Island portion of Acadia National Park, Hancock County (44^0 13' – 44^0 27' North, 68^0 10' – 68^0 26' West), along the mid-coast of Maine. Mount Desert Island was 280 km^2 with 122 km^2 within park boundaries. The landscape consisted of north-south oriented ridges separated by deep U-shaped valleys (Patterson et al. 1983). The highest elevation (466 m) was on the northeast portion of the island at the summit of Cadillac Mountain. Mount Desert Island was situated at the southern limit of the spruce-fir northern hardwoods zone (Westfeld et al. 1956). Soils were dominated by thin, granitic soils (Gilman et al. 1988; Chapman 1970) with organic soils common in wetlands (Calhoun et al. 1994). Palustrine wetlands covered 6% of the island, with most concentrated in the eastern half

of the island. Ponds and lakes covered 4% of the island, 25 of which were greater than 3 ha in area. For the 40 km^2 of palustrine wetlands in Acadia National Park and vicinity (i.e., Mount Desert Island, Schoodic Penninsula, and the surrounding islands): <1% were aquatic bed, 9% were emergent, 48% were forested, 38% were scrub-shrub, and 5% were unconsolidated bottom (Calhoun et al. 1994).

In 1947, a fire burned 69 km^2 of the northeastern portion of Mount Desert Island and subsequent regeneration of vegetation increased the food supply for beaver (*Castor canadensis*), in particular aspen (*Populus* spp.). In turn, this resulted in a dramatic increase in beaver in the park and the creation of extensive networks of wetlands on the east side of the island. Subsequently, food supply for beaver and their populations began to decrease and, thus, many of the current wetlands are abandoned beaver flowages.

<u>Study Site Selection</u>

Potential study sites were identified from National Wetland Inventory maps and smaller, unmapped wetlands that were locally known or that were encountered during preliminary surveys. Study sites were initially selected to represent a gradient for the following variables 1) size of wetland (0.01 – 12.00 ha), 2) dominant cover type (i.e., unconsolidated bottom, aquatic bed, emergent, shrub scrub, or forested), 3) hydrogeomorphic setting (i.e., isolated versus connected to an intermittent or perennial stream), and 4) presence or absence of beaver. I monitored the hydroperiod of 72 wetlands during the 1999 season. Although several of these wetlands contained water year-round, none of the inlets or outlets associated with the sites contained water during the dry part of the summer and, therefore are considered intermittent. Based on 1999 hydroperiod data, I chose for detailed study 21 wetlands (0.01 – 1.58 ha in area) that represent the gradient of wetland permanency, from seasonal wetlands of short flood duration to permanently flooded wetlands. Twenty-two of the 72 sites had fish present; half these sites were dominated by 2 species of small fish: ninespine sticklebacks (*Pungitius pungitius*) and northern redbelly dace (*Phoxinus eos*).

Sampling Methods

Reproductive Effort. To determine reproductive effort of wood frogs and spotted salamanders, I searched the 72 wetlands for egg masses in April 2000 and 2001. I considered all flooded areas of the wetlands less than 1 m in depth as potential egg-laying habitat, although in a few sites spotted salamander egg masses were also recorded in areas up to 1.5 m depth. These searches were done at least once each year and the timing was determined based on local site conditions to maximize the number of egg masses detected for both species. Because I returned to the subset of 21 sites frequently, I continued to monitor for any additional egg masses that were deposited and included those masses in the count.

Hydroperiod Monitoring. Permanent staff gauges constructed of rebar and PVC pipe marked at 5 cm intervals were installed in April 2000. Water levels were recorded approximately bi-weekly at the 72 sites and at least weekly at the subset of 21 sites from April through August 2000 and 2001. For seasonal wetlands, sites were checked more frequently when the site was close to drying to determine actual dry date. All sites that were close to drying by the end of August of 2000 and 2001 were also monitored through October to determine if they subsequently dried.

Pool Characteristics. Several physical pool characteristics that potentially reflected hydroperiod or might otherwise influence breeding population sizes of wood frogs and spotted salamanders at the pools were measured for all 72 sites. Area (m^2) and perimeter (m) of each site were obtained from National Wetland Inventory (NWI) digital ARC/GIS data layers. These measures reflected the area and perimeter of the sites during high water conditions that were typical in early spring. Boundaries of sites that were not on the maps or that differed in size or shape from the mapped configuration were delineated using a global positioning system (position dilution of precision [PDOP] mask = 4.0) and subsequently incorporated into the existing ARC/INFO databases on wetlands coverage. Maximum depth (cm) of each pool was measured in the field during high water conditions. Shallowness of the basin (relative to its perimeter) was measured using the ratio of perimeter to maximum depth of each site. For example, if 2 sites had the same perimeter but differed in the ratio of perimeter to maximum depth, the site with a higher

ratio reflected a site with a shallower basin. I denoted whether an inlet and an outlet were associated with each site, respectively (intermittent or perennial stream present = 1; absent = 0). Each site was classified as to type: 1) upland isolated (a site that has no inlet or outlet associated with it), 2) connected to a stream and small in area (<10,000 m^2), or 3) connected to a stream and large in area ($\geq$10,000 m^2). Hydroperiod category represents the relative length of time that a site will likely contain water in a given year; it is an ordinal categorical variable (range: 1 – 7). These rankings were developed based on day of drying and relative order of drying for the subset of 21 sites in 2000 and 2001; category 1 designates sites that consistently were the first sites to dry in both years and category 7 indicates sites that consistently contain water year-round, even in the most severe drought conditions.

Two additional site characteristics were measured only at the subset of 21 sites. I identified whether a site has unfrozen water present in winter (beneath the surface of the ice) (present = 1; absent = 0). This was measured in the field by drilling through the ice at the deepest area of the pool during February 2001. In May and June 2003, an index of primary productivity was measured during 2 sampling periods of 2 weeks each. Microscope slides were suspended from floats, lengthwise, immediately beneath the surface of the water with 6 slides per float. Six floats (36 slides) were installed at each site during each sampling period. Each float was surrounded on the sides and beneath by window screen mesh to prevent tadpoles (or other algae consumers) from potentially foraging on algae growing on the slides. Floats were randomly placed at near-edge and then far-edge stations, staggered around the perimeter of each pool, to represent all areas less than 1 m in depth. For sites that were large and had deeper areas (> 1 m in depth) in the center of the pool, 2 of the 6 floats were randomly placed in the center area of the pool. Each set of 6 slides had been weighed prior to setting the floats; at the end of each sampling period, sets of slides were dried in an oven and weighed to obtain a measure of algal growth (g). The index of primary productivity was the sum of the difference in the weights (g) for all slides, totaled over the 2 sampling periods. One site dried early in the season and contained water for only the 1st sampling period; for that site, the sum of the difference in weight for the

floats for the 1st sampling period was multiplied by 2, to make the index comparable with the other sites.

Landscape Characteristics. Several landscape setting characteristics that can affect hydroperiod of wetlands and, thus, presumably could influence breeding population sizes of wood frogs and spotted salamanders were measured for all 72 sites. Slope position, percent slope, and catchment area were measured from USGS topographic (7.5 minute series) maps (contour interval: 6 m): slope position denotes whether a site was situated on flat terrain or the lower 1/3 (1), middle 1/3 (2), or upper 1/3 of a major slope (3); percent slope is the percent slope for each site; and, catchment (ha) is the area of land that drains into each site. An index of wetland proximity, the percentage of area within 1000 m of each site covered by wetlands, was calculated using NWI digital ARC/GIS data layers.

Data Analysis

Reproductive Effort. Three categories of reproductive effort for each of the species were designated, based on numbers of egg masses in 2000 for the subset of 21 sites, so that each category contained 7 sites. Specifically, for wood frogs, egg mass categories were: low = <10, medium = 10 – 39, and high = >45 egg masses; for spotted salamanders, egg masses categories were: low = < 55, medium = 55 – 109, and high = >110 egg masses.

To determine if both wood frogs and spotted salamanders breed in the same pools with similar relative frequency, I used a 3 x 3 contingency table analysis, using wood frog egg mass and spotted salamander egg mass categories for the subset of 21 sites. Potential relationships between independent site and landscape variables and wood frog egg mass and spotted salamander egg mass categories were then examined to determine the correlates of these differences. I used Pearson's correlation analysis to evaluate associations between continuous independent site and landscape variables and wood frog egg mass and spotted salamander egg mass categories. Binary independent categorical variables (i.e., presence of an inlet, outlet, or unfrozen water in winter) were converted into proportion of sites that had a value of 1 in each of the 3 egg mass categories for wood frogs and spotted salamanders; these proportions were then

correlated with wood frog egg mass and spotted salamander egg mass categories using Spearman's Rho to test for associations. Kruskal-Wallis tests were used to examine relationships between categorical independent variables that had greater than 2 levels and wood frog egg mass and spotted salamander egg mass categories; ANOVA tests were also used to test these relationships for the categorical independent variables that were ordinal. Scatterplots of all independent site and landscape characteristics were then evaluated to explore potential relationships to wood frog egg mass and spotted salamander egg mass categories as well as counts of wood frog egg masses and spotted salamander egg masses in 2000. Because strong relationships that could be generalized across all sites were not evident, I then explored scatterplots for all site and landscape variables and the response variables (wood frog egg mass category, spotted salamander egg mass category, counts of wood frog egg masses, counts of spotted salamander egg masses) separately for each of the 3 site types in an attempt to isolate factors that may affect only one, but not all of the wetland types. Such interactions would not be easily detected when examining all data together.

Decision Tree Analysis. Many of the scatterplots did not show clear linear trends, but instead contained obvious gaps in the plots at extreme high or low values of the independent variable that were suggestive of factors that act as either negative or positive constraints on egg mass numbers for the species. For each of the 4 response variables (wood frog egg mass category, spotted salamander egg mass category, counts of wood frog egg masses, counts of spotted salamander egg masses), I constructed a series of "If … then …" rule statements to describe potentially constraining effects of independent variables on each of the response variables. For example, "If area of a site is greater than 8,000 m^2, then wood frog egg mass category = L or M". I constructed "If … then …" rules for independent / response variable combinations that showed obvious gaps in the scatterplot.

For each of the 4 response variables, I prepared a separate spreadsheet matrix. "If … then …" rules were represented as rows and the subset of 21 sites as columns. For every rule statement, the corresponding sites that were affected by the rule were marked with the result of the rule. For the example "If area of a site is greater than 8,000 m^2, then wood frog egg mass

category = L or M", cells in that row that correspond to affected sites would be marked with "L or M"; unaffected cells would remain empty. After all the rule statements and the affected cells were entered into the matrix, the sum total of the rules was tallied at the bottom of each column. That is, if all the rules were applied together, what would the proposed number or category of egg mass be for a particular site? For example, if only 3 rules apply to a particular site and 2 rules predicted "L or M" and 1 rule predicted "M or H", the sum total of the rules would be "M". Rows and columns of the matrix were then manipulated to cluster similar sites and rules together. This manipulation allowed me to identify redundant rules, rules whose effects overlapped considerably – but not completely, and rules that were broadly versus narrowly applicable (i.e., applying to many versus few sites). I also prepared separate spreadsheet matrices, as described above, for each of the 3 site types (upland isolated, small sites connected to a stream, and large sites connected to a stream) for each of the 4 response variables.

After arranged the matrices, I constructed 2 separate decision trees for each of the 4 response variables: 1) based on the spreadsheet matrix for all 21 sites and, 2) based on 3 separate matrices, each for one of the site types (upland isolated, connected – small, connected – large) and decision rules corresponding to those sites. The second decision tree was a combination of the results of the 3 site type matrices, with the first nodes separating the sites by site type. These decision trees consisted of a series of "If ... then ..." statements that can be used to predict numbers or category of numbers of egg masses for a given site. Initial "If ... then ..." statements were selected based on my evaluation of what variables best split the clusters of sites. If 2 or more "If ... then ..." statements made the same predictions for a group of sites, but both rules were needed to include the cluster of sites, I used both rules combined. For example, "If area > 10,000 m^2 or perimeter > 400 m, then category of wood frog egg masses = L". I continued to add additional "If ... then ..." rule statements systematically, attempting to use the decision tree to predict the numbers or category of numbers of egg masses for all sites with the highest resolution possible; however, when an "If ... then ..." rule only applied to 1 or 2 sites, I evaluated whether I thought the rule was potentially reasonable or not before including it.

When the decision trees for each of the 4 response variables were completed, I used the remaining category and numbers of egg masses for the 51 sites (averaged over 2000 and 2001) and 2001 data for the subset of 21 sites to test their validity. I used the proportion of correctly classified sites at each step of the decision tree to evaluate strength of evidence of the "If ... then ..." statement.

RESULTS

Reproductive Effort

Wood frogs bred in approximately half of the 72 study sites (37 in 2000 and 39 in 2001); number of egg masses ranged from 0 to 153. In contrast, spotted salamanders bred at nearly all the sites (68 in both 2000 and 2001; 70 in at least one of the study years); number of egg masses ranged from 0 to 913. For the subset of 21 wetlands, number of wood frog egg masses ranged from 0 – 136 and number of spotted salamanders ranged from 4 – 426. The distribution of the 72 study sites (based on the average number of egg masses for 2000 and 2001) for category of wood frog egg masses was low (n = 48), medium (n = 15), and high (n = 9); for category of spotted salamander egg masses, the distribution was low (n = 48), medium (n = 12), and high (n = 12). The distribution of the 21 study sites for category of wood frog egg masses for 2001 was low (n = 7), medium (n = 6), and high (n = 8); for category of spotted salamander egg masses for 2001, the distribution was low (n = 7), medium (n = 8), and high (n = 6).

The ranges of pool characteristics for the 72 sites were: area (116 – 154,267 m^2), perimeter (43 – 2343 m), maximum depth (35 – 206 cm), and ratio of perimeter to maximum depth (0.4 – 18.1) (See Appendix A). Of the 72 sites, 36 had an inlet present and 48 had an outlet present; of the subset of 21 sites, 11 had water present in winter. Of the 72 sites, 23 were upland isolated, 32 were connected to a stream and small in area (<10,000 m^2), and 17 were connected to a stream and large in area ($\geq$10,000 m^2). Ranges of relevant landscape characteristics for the 72 sites were: percent slope (0.05 – 14.29), catchment area (2.03 – 1385.10 ha), and index of wetland proximity (0.58 – 30.72).

Contingency table analysis of wood frog egg mass and spotted salamander egg mass categories showed that wood frogs and spotted salamanders did not select breeding pools with similar relative frequency (X^2 = 3.43, p = 0.49). High numbers of wood frog eggs were associated with 4 pool but no landscape variables; the significant relationships were all characteristic of seasonal wetlands that consistently dry early to mid-summer (P < 0.05). Significant pool variables included: index of primary productivity (r = -0.56), presence of an inlet (r = -0.50), presence of an outlet (r = -0.99), and presence of unfrozen water in winter (r = -0.99). In contrast, high numbers of spotted salamander egg masses were associated with 4 pool but no landscape variables; the significant relationships are all indicative of more permanently flooded wetlands (P < 0.05). Significant pool variables included: presence of an inlet (r = 0.87), presence of an outlet (r = 0.99), presence of unfrozen water in winter (r = 0.98), and hydroperiod category (X^2 = 13.33, p = 0.04). Our results show that although wood frogs and spotted salamanders often breed in the same sites (3 of 21 sites were classified as having high relative importance for both species), the relative order of importance of sites for the 2 species differs (r_s = -0.16, P > 0.05).

Decision Tree Analysis

Category of Reproductive Effort of Wood Frogs. In the decision tree for category of wood frog egg masses (Figure 2.1), 3 of the 4 nodes indicate that sites with long flood duration tend to support fewer wood frog egg masses and all were strongly validated (proportion > 0.85); specifically, sites with larger area, perimeter, maximum depth, or catchment area. The fourth node contained an index of proximity to wetlands, and, thus, is an indirect measure of the isolation of a site from other potential breeding sites; however, this node is not well supported by validation (proportion = 0.50). The decision tree for category of wood frog egg masses that treats site type separately was more complicated (Figure 2.2). For both small and large sites connected to a stream, each have 1 node that either directly or indirectly indicates that sites with long flood duration have fewer wood frog egg masses and were strongly validated (proportion > 0.90); specifically, sites with longer hydroperiod and larger maximum depth. The other nodes (5 and 7) in Figure 2.2, for both small and large sites connected to a stream, are less easily interpreted and

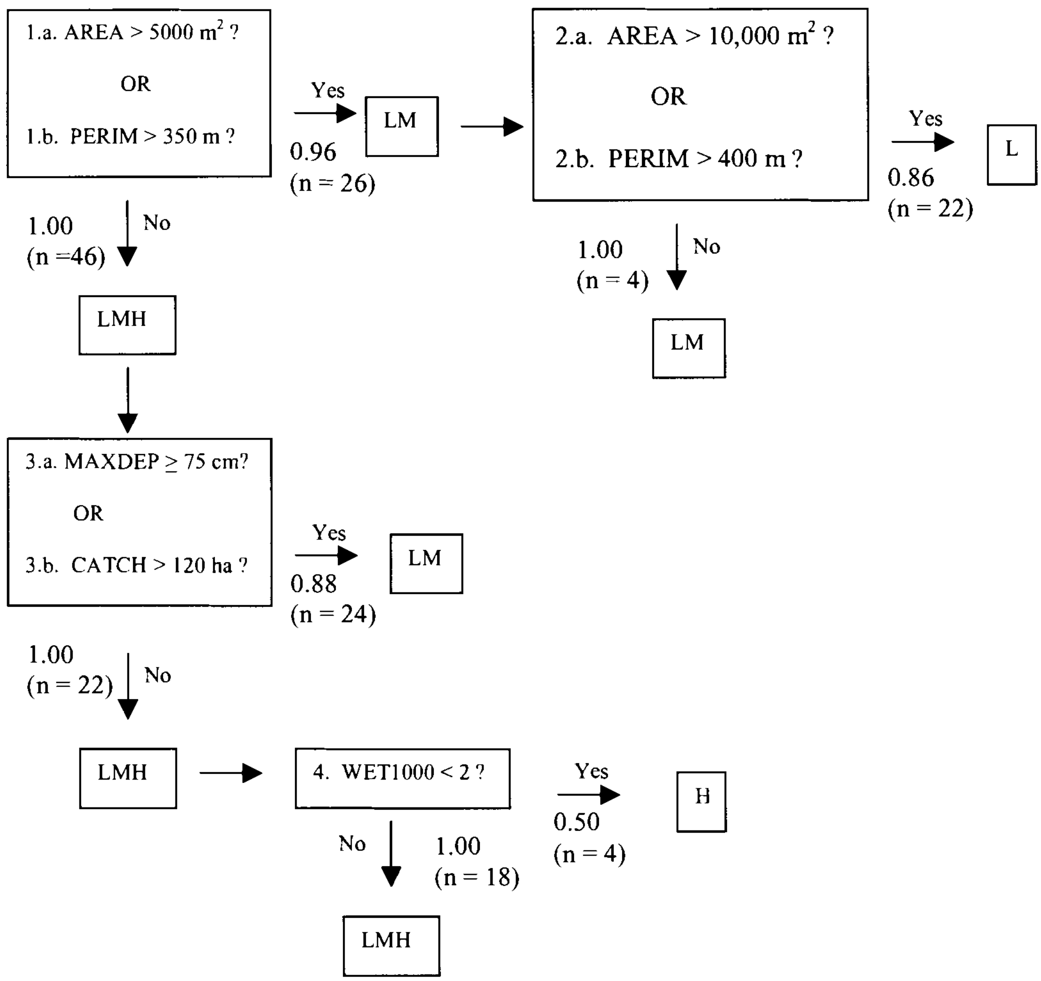
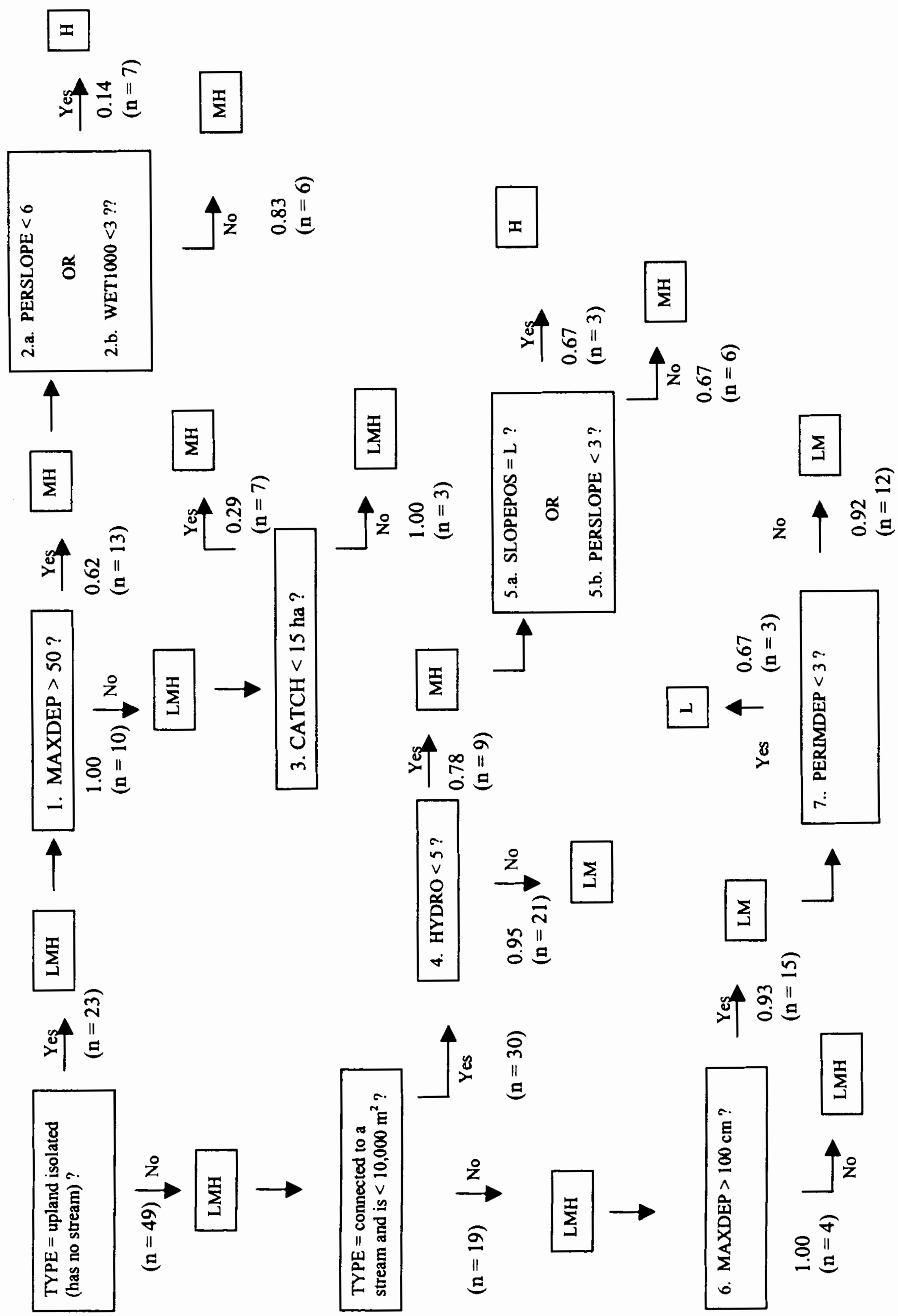


Figure 2.1. Decision tree for category of reproductive effort for wood frogs based on numbers of egg masses for 21 wetlands in Acadia National Park in 2000. The proportion of validation sites (n = 72) that were classified correctly is shown at each node; the sample size is in parentheses. Key: AREA = area of the pool (m^2), PERIM = perimeter of the pool (m), MAXDEP = maximum depth (cm), CATCH = area of land that drains into the site (ha), WET1000 = index of wetland proximity, L = < 10 egg masses, M = 10 – 39 egg masses, H = > 39 egg masses.

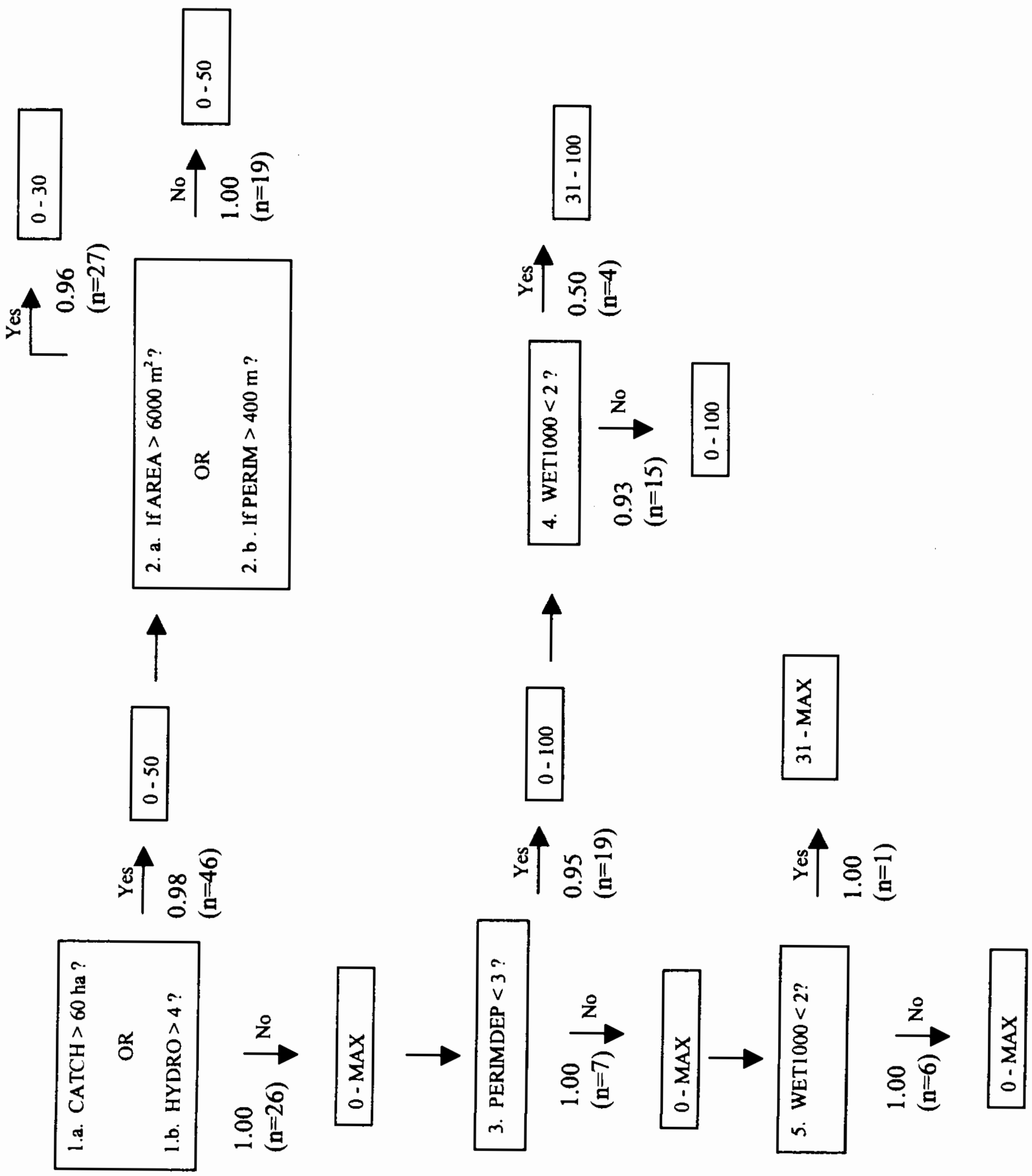


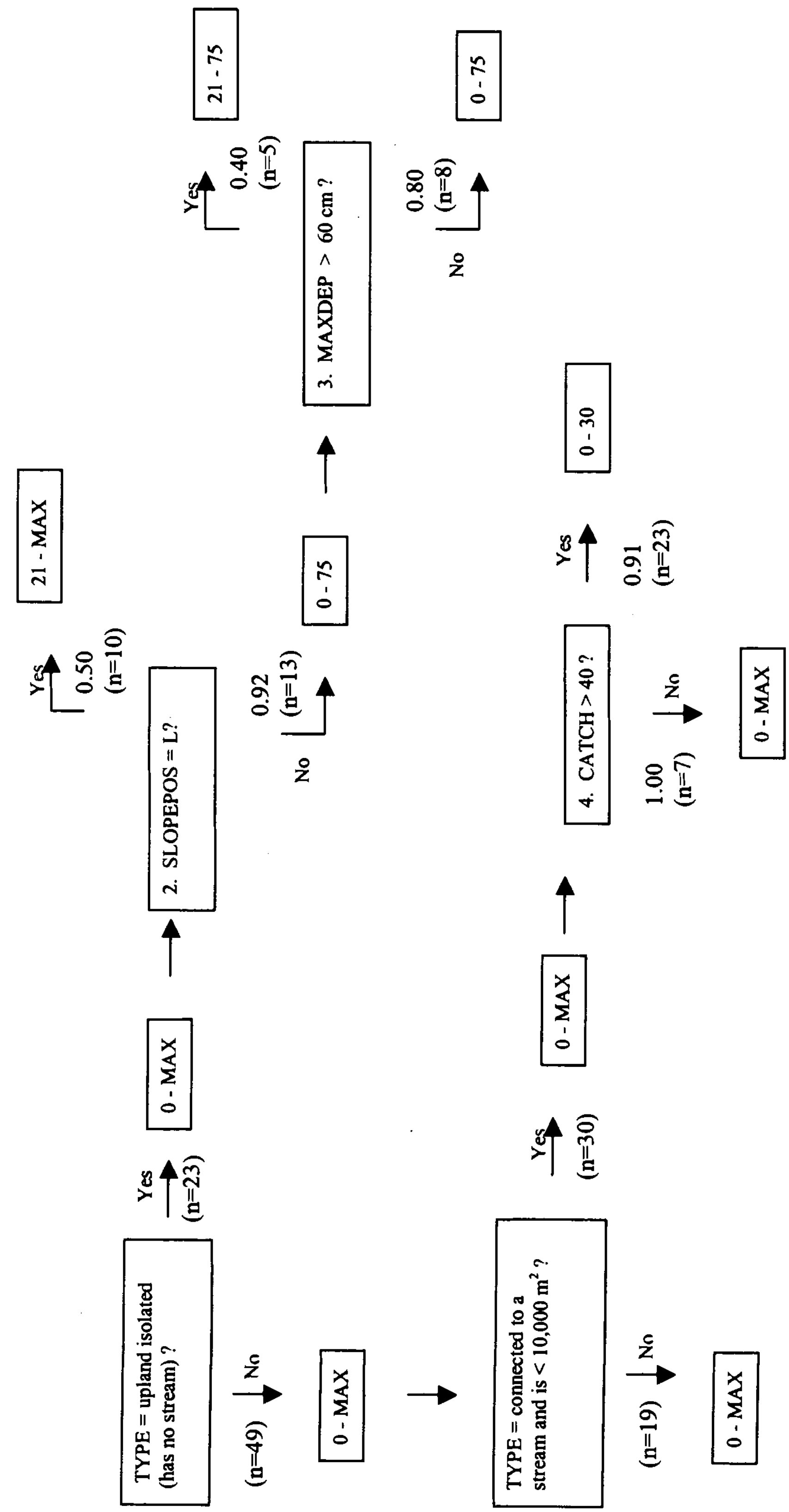
TYPE = upland isolated (has no stream) ?
Yes
(n = 23)
LMH
1. MAXDEP > 50 ?
Yes
0.62
(n = 13)
MH
2.a. PERSLOPE < 6
OR
2.b. WET1000 <3 ??
Yes
0.14
(n = 7)
H
No
0.83
(n = 6)
MH
No
1.00
(n = 10)
LMH
3. CATCH < 15 ha ?
Yes
0.29
(n = 7)
MH
No
1.00
(n = 3)
LMH
No
(n = 49)
LMH
TYPE = connected to a stream and is < 10,000 m² ?
Yes
(n = 30)
4. HYDRO < 5 ?
Yes
0.78
(n = 9)
MH
5.a. SLOPEPOS = L ?
OR
5.b. PERSLOPE < 3 ?
Yes
0.67
(n = 3)
H
No
0.67
(n = 6)
MH
No
0.95
(n = 21)
LM
No
(n = 19)
LMH
6. MAXDEP > 100 cm ?
Yes
0.93
(n = 15)
LM
7.. PERIMDEP < 3 ?
Yes
0.67
(n = 3)
L
No
0.92
(n = 12)
LM
No
1.00
(n = 4)
LMH

are not well supported (proportion < 0.70). Nodes for upland isolated sites did not show clear relationships between flood duration of wetlands nor other potential driving factors and numbers of wood frog egg masses; none of the nodes is well supported (proportion < 0.65).

Number of Wood Frog Egg Masses. In the counts of wood frog egg masses decision tree for all site types (Figure 2.3), 2 of the 5 nodes represent 4 independent variables that suggest that wetlands of long flood duration have characteristics that act to limit the number of wood frog egg masses and are well validated; specifically, nodes with larger pool area or perimeter, catchment area, and longer hydroperiod. One well-validated node (proportion = 0.95) indicates that sites with steep basins (i.e., low values of the ratio of perimeter to maximum depth) may also act as a constraint on numbers of egg masses. Wetlands with low ratios of perimeter to maximum depth are typically small and very deep; this could contribute to longer flood duration as compared to other small wetlands. The last 2 nodes contained an index of proximity to wetlands, but these nodes are either poorly validated (proportion = 0.50) or only had 1 site to validate it and, thus, are not well supported. In the decision tree that treats site type separately (Figure 2.4), small sites that are connected to a stream that have large catchment areas – and, presumably longer flood duration – likely constrain the maximum number of egg masses; this node is well validated (proportion = 0.91). Nodes for upland isolated sites (containing slope position and maximum depth as independent variables) generally failed to be validated, except that mid to upper slope did indicate a possible constraint on numbers of egg masses (proportion = 0.92), which is not easily explained. Numbers of wood frog egg masses for large sites connected to a stream are not predictable in this decision tree.

Category of Reproductive Effort of Spotted Salamanders. In the category of spotted salamander egg masses decision tree for all site types (Figure 2.5), all 3 nodes have independent variables (specifically, long hydroperiod and large catchment area) that either directly or indirectly lengthen the flood duration of wetlands and suggest somewhat contradictory results. One node indicates that longer hydroperiod may result in a higher category of spotted salamander egg masses, yet this node is not well validated (proportion = 0.34). In contrast, the other 2 nodes indicate that larger catchment area reflect lower category of spotted salamander egg masses;


1.a. CATCH > 60 ha ?
OR
1.b. HYDRO > 4 ?
Yes
0.98
(n=46)
0 - 50
2. a. If AREA > 6000 m² ?
OR
2. b. If PERIM > 400 m ?
Yes
0.96
(n=27)
0 - 30
No
1.00
(n=19)
0 - 50
No
1.00
(n=26)
0 - MAX
3. PERIMDEP < 3 ?
Yes
0.95
(n=19)
0 - 100
4. WET1000 < 2 ?
Yes
0.50
(n=4)
31 - 100
No
0.93
(n=15)
0 - 100
No
1.00
(n=7)
0 - MAX
5. WET1000 < 2?
Yes
1.00
(n=1)
31 - MAX
No
1.00
(n=6)
0 - MAX


TYPE = upland isolated (has no stream) ?
Yes
(n=23)
0 - MAX
2. SLOPEPOS = L?
Yes
0.50
(n=10)
21 - MAX
No
0.92
(n=13)
0 - 75
3. MAXDEP > 60 cm ?
Yes
0.40
(n=5)
21 - 75
No
0.80
(n=8)
0 - 75
No
(n=49)
0 - MAX
TYPE = connected to a stream and is < 10,000 m^2 ?
Yes
(n=30)
0 - MAX
4. CATCH > 40 ?
Yes
0.91
(n=23)
0 - 30
No
1.00
(n=7)
0 - MAX
No
(n=19)
0 - MAX

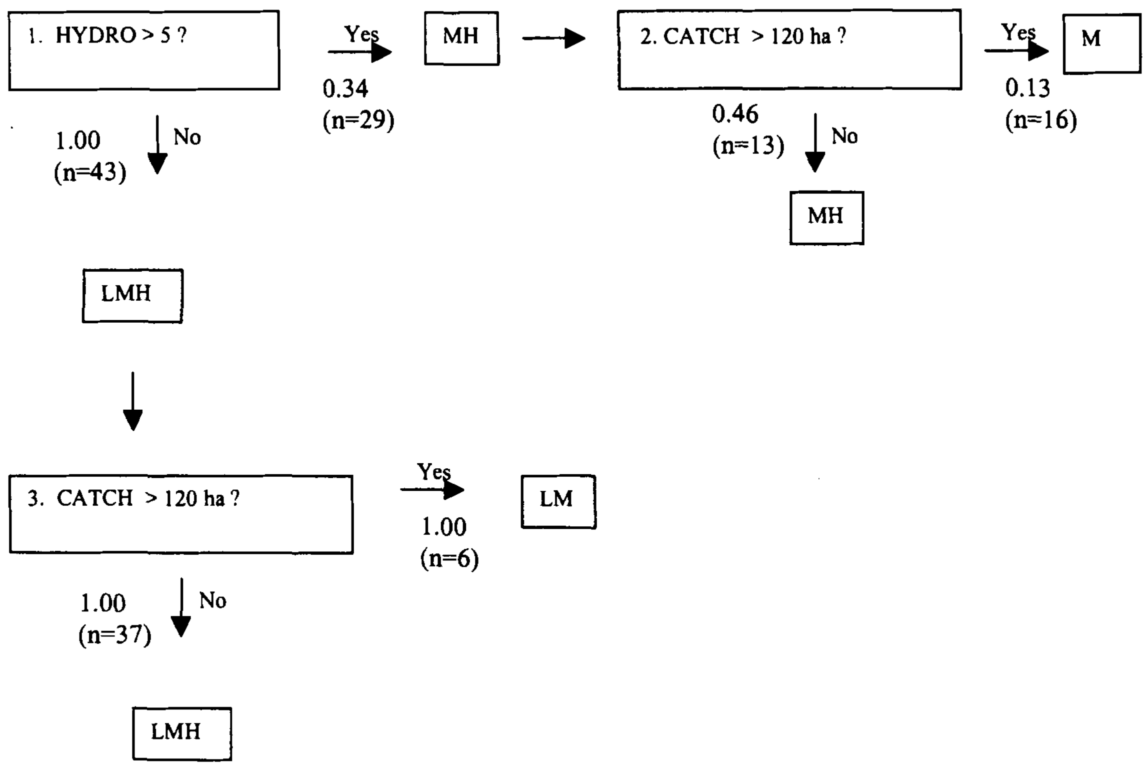
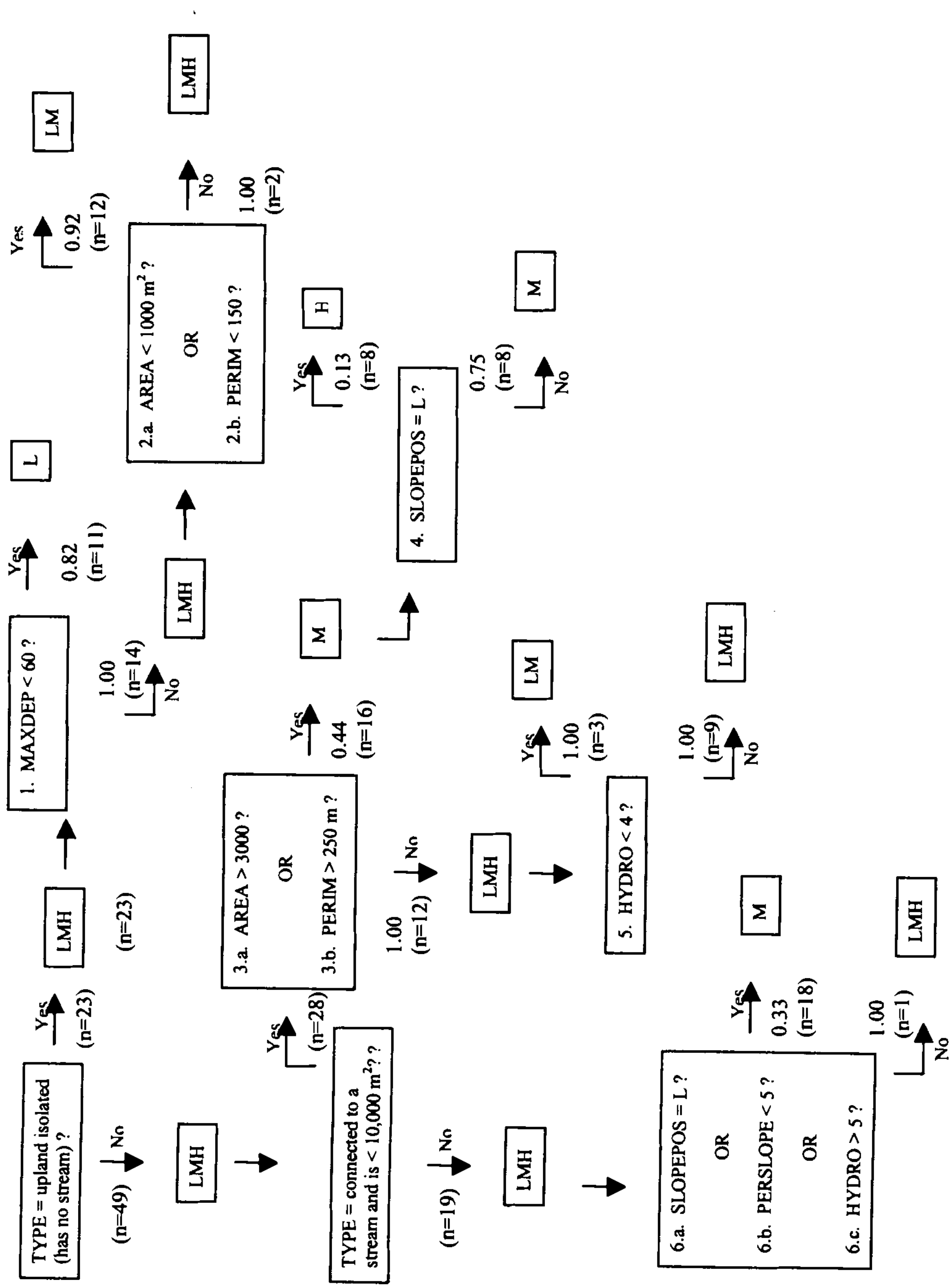


Figure 2.5. Decision tree for category of reproductive effort for spotted salamanders based on numbers of egg masses for 21 wetlands in Acadia National Park in 2000. The proportion of validation sites (n = 72) that were classified correctly is shown at each node; the sample size is in parentheses. Key: HYDRO = hydroperiod category (1 = shortest, 7 = longest), CATCH = area of land that drains into the site (ha), L = < 55 egg masses, M = 55 – 109 egg masses, H = > 109 egg masses.

however, the validation process only supports one of these nodes. In the decision tree that treats site type separately (Figure 2.6), nodes for upland isolated sites contain independent variables (smaller pool area, perimeter, and maximum depth) that indicate wetlands with short flood duration likely limit the number of breeding spotted salamanders; the validation test supported this (proportion > 0.80). Similarly, for small sites connected to a stream, 2 nodes that contain variables (larger pool area and perimeter and lower slope position) associated with long flood duration of wetlands supported higher categories of spotted salamander egg masses, but are not well validated (proportion < 0.50). The other node, which represents sites that are small in pool area or perimeter and short in flood duration, had lower categories of spotted salamander egg masses; this node is not well validated (proportion = 1.00, but with only 3 test sites). Large sites connected to a stream had 1 node with 3 independent variables that could be associated with length of flood duration, specifically, lower slope position, smaller percent slope, or longer hydroperiod. This node could be interpreted as indicating that large sites connected to a stream have characteristics that directly or indirectly lengthen the flood duration of wetlands; in turn, this will tend to support higher categories of spotted salamander egg masses. This node, however, is not well supported by the validation (proportion = 0.33).

Number of spotted salamander egg masses. The decision tree for counts of spotted salamander egg masses for all site types contained only 2 nodes (Figure 2.7); the first node indicates that sites with shallow-sided basins (i.e., larger ratios of perimeter to maximum depth) support larger numbers of egg masses. This node, however, lacks strong support (proportion = 0.44). The second node indicates that sites with steeper basins (i.e., smaller ratios of perimeter to maximum depth) and larger catchment area may limit the number of egg masses; steeper basins may reflect a lack of egg deposition or larval habitat at those sites. In the decision tree for counts of spotted salamander egg masses that treats site type separately (Figure 2.8), for upland isolated sites, 3 of the 4 nodes contain variables (i.e., smaller pool area, perimeter, or maximum depth) that are typical of wetlands of short flood duration, thus indicating that these conditions constrain numbers of egg masses; these nodes are well validated (proportion $\geq$0.75). For small sites connected to a stream, 2 of the 3 nodes have 2 independent variables that suggest that


TYPE = upland isolated (has no stream) ?
Yes
(n=23)
LMH
(n=23)
1. MAXDEP < 60 ?
Yes
0.82
(n=11)
L
1.00
(n=14)
No
LMH
2.a. AREA < 1000 m² ?
OR
2.b. PERIM < 150 ?
Yes
0.92
(n=12)
LM
No
1.00
(n=2)
LMH
(n=49)
No
LMH
TYPE = connected to a stream and is < 10,000 m²? ?
Yes
(n=28)
3.a. AREA > 3000 ?
OR
3.b. PERIM > 250 m ?
Yes
0.44
(n=16)
M
4. SLOPEPOS = L ?
Yes
0.13
(n=8)
H
0.75
(n=8)
No
M
1.00
(n=12)
No
LMH
5. HYDRO < 4 ?
Yes
1.00
(n=3)
LM
1.00
(n=9)
No
LMH
(n=19)
No
LMH
6.a. SLOPEPOS = L ?
OR
6.b. PERSLOPE < 5 ?
OR
6.c. HYDRO > 5 ?
Yes
0.33
(n=18)
M
1.00
(n=1)
No
LMH

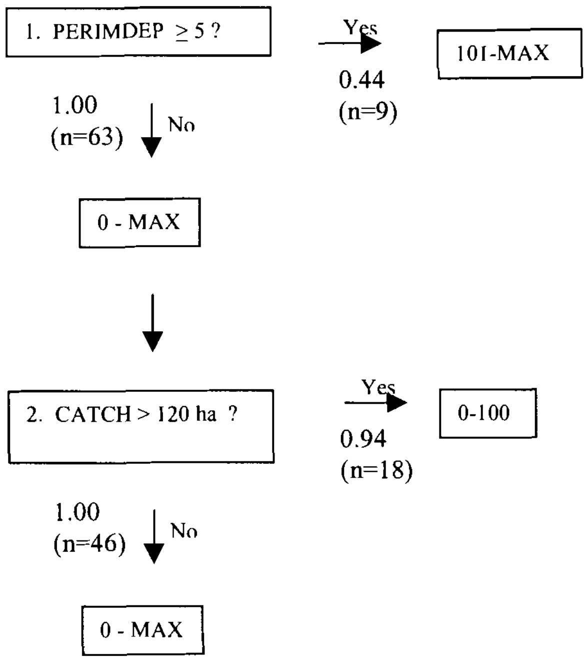
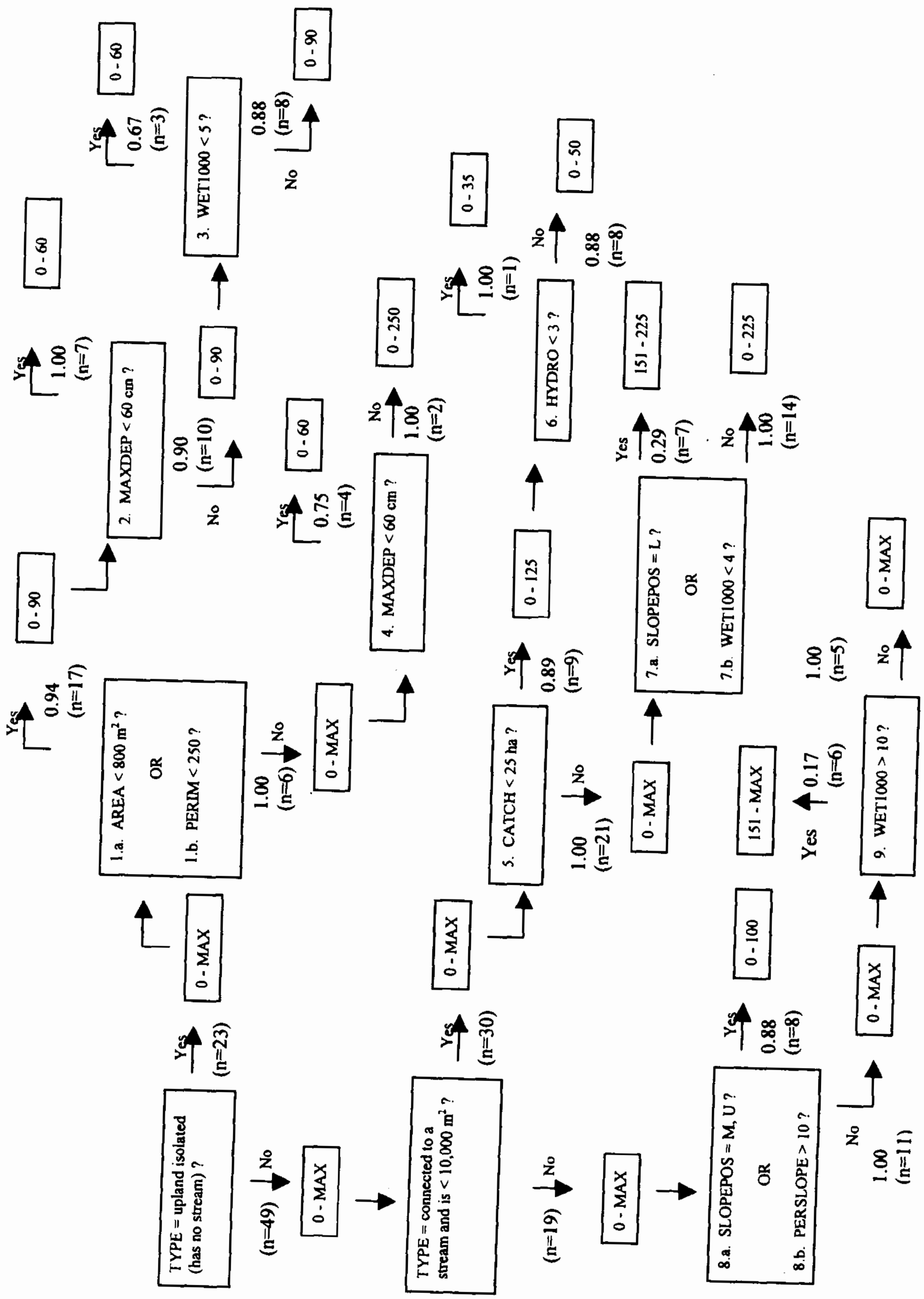


Figure 2.7. Decision tree for number of spotted salamander egg masses based on numbers of egg masses for 21 wetlands in Acadia National Park in 2000. The proportion of validation sites (n=72) that were classified correctly is shown at each node; the sample size is in parentheses. Key: PERIMDEP = ratio of the perimeter to maximum depth of the pool, CATCH = area of land that drains into the site (ha), MAX = unlimited number of egg masses.

Figure 2.8. Decision tree for category of number of spotted salamander egg masses, that treats site type separately, based on numbers of egg masses for 21 wetlands in Acadia National Park in 2000. The proportion of validation sites (n=72) that were classified correctly is shown at each node; the sample size is in parentheses. Key: TYPE = site type, AREA = area of the pool (m^2), PERIM = perimeter of the pool (m), MAXDEP = maximum depth of the pool (cm), WET1000 = the percentage of area within 1000 m radius of each site, covered by wetlands, CATCH = area of land that drains into the site (ha), HYDRO = hydroperiod category (1 = shortest, 7 = longest), SLOPEPOS = slope position of the site (1 = flat terrain or lower 1/3, 2 = middle 1/3 of slope, 3 = upper 1/3 of slope), PERSLOPE = percent slope, MAX = unlimited number of egg masses.


TYPE = upland isolated (has no stream) ?
TYPE = connected to a stream and is < 10,000 m² ?
1.a. AREA < 800 m² ? OR 1.b. PERIM < 250 ?
2. MAXDEP < 60 cm ?
3. WET1000 < 5 ?
4. MAXDEP < 60 cm ?
5. CATCH < 25 ha ?
6. HYDRO < 3 ?
7.a. SLOPEPOS = L ? OR 7.b. WET1000 < 4 ?
8.a. SLOPEPOS = M, U ? OR 8.b. PERSLOPE > 10 ?
9. WET1000 > 10 ?

sites with short flood duration act to limit numbers of egg masses (i.e., smaller catchment area and shorter hydroperiod); these nodes are supported by validation (proportion > 0.85). The third node suggests that lower slope position, which could lengthen the flood duration of a site, supports higher egg mass numbers, although this node is not well supported by validation (proportion < 0.30). For large sites connected to a stream, the 2 nodes suggest that mid and upper slope position or sites positioned on steeper slopes may limit numbers of egg masses; this node is supported by validation (proportion > 0.85).

DISCUSSION

Although wood frogs and spotted salamanders have both been assumed to rely on seasonal pools for greatest breeding success (Tappan 1997; Calhoun 2003; Hunter et al. 1999), my findings indicate that they typically differ in which pools have highest breeding population sizes. This is consistent with other amphibian studies that indicate that species differ as to the hydroperiod of wetlands that is most suitable for successful reproduction (Pechman et al. 1989, Rowe and Dunson 1995, Semlitsch et al. 1996, Babbit and Tanner 2000, Semlitsch 2000). Specifically, my results indicate that wood frogs were associated with sites that lack a connection with a stream, lack unfrozen water in winter, and dry early in the summer, whereas spotted salamanders had the opposite relationships with these variables. Because wood frogs can metamorphose much earlier than spotted salamanders in a given year (Kolozsvary unpublished data, Paton and Crouch 2002), the contrasting relationship of these variables for the 2 species is reasonable. Wood frogs were not as well distributed across the landscape as spotted salamanders; they were recorded breeding at approximately half the sites, whereas spotted salamanders were documented breeding in 70 of the 72 sites in at least one of the study years.

<u>Wood Frogs</u>. Consistent with my predictions, low numbers of wood frog egg masses were most common in wetlands of long flood duration or associated characteristics, specifically, larger pool area, perimeter, maximum depth, and catchment area. In addition, high numbers of egg masses were associated with lower primary productivity, which may be characteristic of

seasonal wetlands of short flood duration. Wood frogs are believed to rely on seasonal pools for successful breeding because of decreased predation pressure, as compared to permanent wetlands that have substantial predator communities, especially fish predators (Tappan et al., Calhoun 2003). I was not, however, able to predict high numbers of wood frog egg masses with great success. Apparently, these factors can limit the potential breeding population size at a site, but are not good at predicting absolute numbers. Instead, maximal breeding population size is constrained by the factor that most severely limits the population size at that particular location (see O'Connor 2002). There are several possible factors that affect population size of wood frogs. For example, wood frogs have a biphasic life cycle and they use forested habitats outside the breeding season (Tyning 1990, Hunter et al. 1999) thus characteristics of the surrounding landscape will also affect breeding population size, beyond their influence on hydroperiod (Dodd and Cade 1998, Semlitsch 1998, Guerry and Hunter 2002). Furthermore, biotic influences (e.g., competition, predation) have been shown to interact with hydroperiod to influence the reproductive success of pond-breeding amphibians as well as the overall structure of amphibian communities (Wilbur 1987, Pechman et al. 1989, Rowe and Dunson 1995).

There was a notable exception to the contention that larger wetlands and longer flood duration limits numbers of wood frog egg masses. One of the 51 validation sites (East of Fawn Pond) was large in size (29,688 m^2) and had a long flood duration (i.e., only would dry in extreme drought conditions), yet had the highest numbers of wood frog egg masses of all the 72 sites (i.e., 153 egg masses in 2001). This site was positioned on the upper 1/3 of a slope and had a relatively small catchment area. The site was fishless, probably because the intermittent outlet was situated on a steep slope that served as a barrier to the movement of fish. Fish predation has been considered one of the important factors affecting survival of many amphibian larvae (Petranka 1983, Ireland 1989, Tyler et al. 1998a, Tyler et al. 1998b), including wood frogs (Hopey and Petranka 1994). Reduced predation pressures at such a site could result in large breeding population sizes of wood frogs, contrary to my initial predictions and the decision trees based on physical parameters.

Spotted Salamanders. Decision trees for spotted salamanders provided weaker evidence for my predictions than the decision trees for wood frogs. As with wood frogs, they appeared to best predict conditions that limit the breeding population sizes. This was particularly evident in the decision trees that dealt with the site types separately. For upland isolated sites, factors that contribute to short flood duration (smaller pool area, perimeter, and maximum depth) all indicated a limit, or constraint, on the numbers of egg masses. Because of the relatively long egg and larval development times of ambystomid salamanders, this appears reasonable (Hunter et al. 1999, Paton and Crouch 2002). Numbers of spotted salamander egg masses at other types of sites (those connected with a stream) or upland isolated sites with high numbers were less predictable. As for wood frogs, spotted salamanders have a biphasic life cycle and use forested areas outside the breeding season, and thus features of the surrounding landscape affect breeding population size as well (Windmiller 1996, Semlitsch 1998, Guerry and Hunter 2002). In addition, because spotted salamanders are longer-lived than wood frogs (Tyning 1990, Hunter et al. 1999) and have more opportunities to breed in their lifetime, they may be able to exploit wetlands in which reproduction fails in most years. It has been shown that many pool-breeding amphibians have only occasional years of successful reproduction, yet sustain breeding populations at these sites (Pechman et al. 1989, Semlitsch et al. 1996). If individual sites only occasionally have the appropriate hydroperiod for a given species to successfully reproduce, then it may be difficult to differentiate between pool and landscape characteristics of productive versus marginal sites.

Of the subset of 21 sites, 1 site (HQVP) is an exception to the argument that wetlands of short flood duration constrain the breeding population size of spotted salamanders; it was one of the first sites to dry each year, yet contained more than 200 spotted salamander egg masses. This site was also very isolated from other potential breeding sites (>500 m) and, thus, it is unlikely that it is populated solely from dispersing individuals. I suspect that if the precipitation and temperature patterns are favorable in a given year, this site could produce high numbers of metamorphs, thus offsetting typical years in which the site dries prior to metamorphosis. In

contrast, I suspect that more permanently flooded sites that predictably contain water in most years may be more stable in terms of consistently producing metamorphs.

Connectivity of Breeding Sites. Connections between breeding populations of pond-breeding amphibians is thought to be important for maintaining metapopulations or occupancy of breeding ponds (Sjogren 1990, Kolozsvary and Swihart 1999, Marsh and Trenham 2001). However, proximity to wetlands and thus to potential sources of dispersing metamorphs did not prove to be important in the decision tree analysis; nodes with this variable were not well supported. A caveat with this metric is that the potential significance of proximity to wetlands could work in two different ways. Specifically, high proximity to wetlands could be important in providing a source population for individuals that colonize or re-colonize vacant sites or reproductive sinks (Sjogren 1991). In contrast, low proximity to wetlands could mean that individuals dispersing from these sites exhibit high natal philopatry because they do not encounter other potential breeding sites. High proximity to wetlands certainly has the potential to be important in sustaining metapopulations of wood frogs and spotted salamanders, but this concept is not supported by this study.

High Population Sites Shared by Both Species. Of the subset of 21 sites, 3 sites had high numbers of both wood frog and spotted salamander egg masses, but they generally were not similar in most of the pool or landscape metrics I measured, except that 2 of the 3 sites are well isolated from other potential breeding areas. One site (HQVP) was described above. The second site (Bubble middle) typically dries in late summer or early autumn or holds water year-round and is large, relatively shallow, and has an intermittent inlet and 2 outlets; flood duration is prolonged at this site, likely a result of a large, precipitous rocky catchment. It also is well isolated from other potential breeding areas and at the base of 2 precipitous mountains, which may lead to metamorphs exhibiting higher natal philopatry (as previously discussed). This site is choked with emergent vegetation. Two striking attributes that may contribute to the high numbers of breeding wood frogs and spotted salamanders may be that the vegetation provides abundant escape and foraging opportunites for the larvae. The third site (MB's FAV) is very large, deep, and has an intermittent outlet, and consistently dried in mid to late summer each year; this site

probably provides a relatively consistent flood duration from year to year that is favorable for both wood frogs and spotted salamanders.

Brooks and Hayashi (2002) investigated the relationship between morphometric parameters and hydroperiod of 34 vernal pools in central Massachusetts. They found weak correlations between the variables and hydroperiod, with the strongest relationship between maximum pool volume and hydroperiod. In general, they found that pools that were either deep, large in area, or large in volume had longer hydroperiods, yet pools that were shallow, small in area, or small in volume had varying hydroperiods. Skidds and Golet (2003) examined site characteristics (including pool morphometry, water chemistry, geologic setting, and canopy cover) and hydroperiods of 65 seasonal pools in southern Rhode Island and reported that canopy cover, pool depth, and specific conductance were good predictors of ponds with suitable hydroperiods for reproduction by wood frogs and spotted salamanders. Furthermore, they identified several plant species as potential indicators, as well. These studies, as well as my own, indicate that predicting suitable hydroperiods for reproduction by wood frogs and spotted salamanders may be difficult if based solely on pool and landscape characteristics, because hydroperiod may also be affected by patterns of precipitation, evapotranspiration, and ground-water exchange (Mitsch and Gosselink 2000).

Summary. This study reinforces the idea that several factors affect the relative importance of individual wetlands as potential breeding sites for wood frogs and spotted salamanders and that none are good at predicting absolute numbers. These factors act to constrain breeding population size, and the most severely limiting factor will ultimately dictate maximal breeding population size at the individual sites. Physical pool variables that influence hydroperiod, and thus affect the breeding potential for amphibian species, include pool area and perimeter, maximum depth, and presence or absence of an inlet, outlet, or unfrozen water in winter. Surrounding landscape variables, such as the size of the catchment area of a breeding pool, somewhat affected breeding potential for these species, but were not as influential as the pool characteristics. In general, spotted salamanders bred in wetlands with various hydroperiod characteristics (i.e., seasonal wetlands of long flood duration, permanently flooded wetlands with

non-predaceous fish, seasonal wetlands of short flood duration if the sites periodically contain water for a sufficient duration to allow metamorphosis), although highest breeding numbers were associated with wetlands of long flood duration. In contrast, wood frogs had a restricted distribution and had greatest breeding populations in seasonal wetlands of short flood duration. Both species did not generally breed in high numbers at the same sites and the few sites that did share high numbers of both species did not have similar hydrological characteristics.

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Chapter 3

AN EVALUATION OF POND SAMPLING TECHNIQUES FOR LARVAL AMPHIBIANS IN WETLANDS

ABSTRACT

A common objective of many aquatic amphibian studies involves documenting the presence or species richness of larval amphibians at breeding pools. Although several techniques are commonly employed for sampling larval amphibians, a side-by-side comparison of their efficiency at documenting species presence or in capturing individuals is not often assessed. I used 4 larval sampling techniques (dip nets, pipe samplers, funnel traps, and bottle traps) to sample amphibian larvae in 30 wetlands in July and August 1999. For the 4 focal species (i.e., spotted salamanders [*Ambystoma maculatum*], eastern newts [*Notophthalmus viridescens*], green frogs [*Rana clamitans*], and bull frogs [*Rana catesbeiana*]), funnel traps had the highest probability of detection for a given level of effort (i.e., number of stations). For spotted salamanders and bull frogs, dip nets were the least effective; for eastern newts, bottle traps performed the poorest; and for green frogs, pipe samplers and bottle traps had the lowest probability of detection for a given level of effort. Green frog larvae had the highest probability of detection and spotted salamanders had the lowest for all 4 techniques. The mean number of person hours per station was lowest for dip nets and was similar for pipe samplers, funnel traps, and bottle traps. In terms of numbers of individuals captured, funnel traps generally captured the most spotted salamanders and bull frogs. For eastern newts, pipe samplers captured the most individuals whereas for green frogs, pipe samplers and funnel traps typically captured the most individuals. Dip nets and bottle traps typically yielded the lowest numbers of individuals across species.

INTRODUCTION

For amphibians that rely on wetlands for breeding, a question that is often asked is whether a target species actually breeds in a given wetland? Call surveys are frequently used to document anuran breeding, but this technique can be misleading because anurans often vocalize at sites in which they are known not to breed (personal observation) or in which reproduction is unsuccessful and some species have such a short breeding period that vocalization could be missed. Larval surveys take more time to implement than call surveys, but they 1) document actual breeding of species, 2) can provide an index of reproductive success at some point of larval development, and 3) document non-calling amphibians such as salamanders.

Several techniques are commonly used to sample larvae (see reviews of methods by Olson et al. 1997, Shaffer et al. 1994), but their efficiency is rarely investigated (e.g., Buech and Egeland 2002a and 2002b). Local and regional differences in the assemblage of larval amphibians or the physical characteristics of the wetlands may also warrant the use of different techniques. For example, in wetlands with clear water or minimal vegetation, active sampling techniques that use visual cues (e.g., visual counts, snorkeling) may be warranted, whereas these techniques would not be suitable for vegetation-choked or murky waters.

The purpose of this study was to compare 4 larval sampling techniques in terms of detecting species presence, determining species richness, and capturing numbers of individuals of a given species. I sampled larval amphibians in 30 wetlands in Acadia National Park, Maine, USA in July and August 1999. I examined the probability of capture of common species for the 4 techniques and used that information to determine the time required to implement each technique, as well as its effectiveness in determining species richness, for a given level of effort. I calculated the minimum number of stations required to document the presence of individual species, with a probability of 90%. I also examined the mean numbers of individuals captured per station for each of the techniques across all wetlands.

METHODS

Study Area

The study area is located along the mid-coast of Maine, USA, on the Mount Desert Island portion of Acadia National Park, Hancock County (44^0 13' – 44^0 27' North, 68^0 10' – 68^0 26' West). The terrain of Mount Desert Island consists of north-south oriented ridges separated by deep U-shaped valleys (Patterson et al 1983). The highest elevation (466 m) is on the northeast portion of the island at the summit of Cadillac Mountain. Mount Desert Island is situated at the southern limit of the spruce-fir northern hardwoods zone (Westfeld et al. 1956). Uplands are dominated by thin, granitic soils (Gilman et al. 1988; Chapman 1970) with organic soils common in wetlands (Calhoun et al. 1994). Six percent of the island contains palustrine wetlands, with most concentrated in the eastern half of the island. Ponds and lakes cover 4% of the island, 25 of which are greater than 3 ha in area. For the 40 km^2 of palustrine wetlands in Acadia National Park and vicinity (i.e., Mount Desert Island, Schoodic Penninsula, and the surrounding islands): <1% are aquatic bed, 9% are emergent, 48% are forested, 38% are scrub-shrub, and 5% are unconsolidated bottom (Calhoun et al. 1994). Beaver-created wetlands, both occupied and abandoned, are common, particularly on the east side of the island. Wetland conditions vary from oligotrophic sites with gravel substrates and sparse vegetation to eutrophic sites with muck substrates and abundant vegetation. Most wetlands are dystrophic, with tannin-stained waters, and thus the visibility in the water column is generally low.

Study Site Selection

Potential study sites were identified from palustrine wetlands, less than 15 ha in area, on National Wetland Inventory (NWI) maps and from among smaller, unmapped wetlands that were known to exist or that were encountered during preliminary surveys as part of a larger study (See Chapters 1 and 2). Wetland study sites were initially selected randomly, stratified on: 1) size of wetland (0.01 – 15.00 ha), 2) dominant wetland class (based on the Cowardin classification system [1979]), 3) hydrogeomorphic setting (i.e., isolated versus connected to a stream), and 4)

presence/absence of beaver. Seventy-two wetlands were monitored in 1999 as part of a larger study; the sites ranged in duration of flooding from seasonal wetlands of short duration to permanent wetlands. Thirty sites still contained water in July and August 1999 and were sampled for this study. The sites were generally limited to larger wetlands, with some semi-permanent or permanent smaller wetlands; size range for sites during basin-full, spring conditions was 0.05 – 15.00 ha. Twenty-five sites were influenced by an active or abandoned beaver dam and channels.

Sampling Methods

The 30 wetlands were separated into 5 groups with 4 – 8 sites per group; sites were grouped by location, so that travel time between sites would be minimized. Each group was sampled for 6 consecutive days between 12 July and 10 August 1999. Potential larval habitat was considered all areas of standing water that were less than 1 meter depth, yet deep enough to allow sampling equipment to be fully submerged. On the first sampling day for each group, sampling stations were established throughout potential larval habitat. For large wetlands that had similar vegetation on two sides, sampling stations were established only on one side to reduce sampling time. In large sites with broad areas of potential larval habitat along the edge, stations were staggered alternately, with one near-edge station, followed by one far-from-edge station. The number of stations sampled was based on the the approximate area of potential larval habitat at a particular wetland to keep sampling effort in proportion to area.

Four techniques were used at each station at each wetland: 2 active sampling techniques (dip nets and pipe samplers) and 2 passive sampling techniques (funnel traps and bottle traps). A consecutive 6-day sampling period consisted of: 1 day dip-net sampling, 1 day pipe sampling, 4 days simultaneously funnel trapping and bottle trapping (1st day consisted of setting the traps, and then 3 days of checking the traps). The order of the sampling days varied across the sites (although funnel and bottle trapping were always conducted on consecutive days). At each station 3 pipe and 2 dip net samples were taken; fewer dip nets were taken in an effort to sample similar volumes of water. At each station, both a funnel and bottle trap were established. I also

recorded the number of person hours it took to sample each site with each of the four techniques; this included set up time as well as actual sampling time.

Dip Nets. Dip nets were 'D" shape, 30.5 cm diameter (i.e., maximum width) and depth 20.1 cm; sides of net were made of heavy cotton and nylon canvas with a 500 micron mesh bottom. Two dip net sweeps, approximately 3 meters apart, were taken at each station. Each sweep began at the top of the water column in front and slightly to the side of the observer; the net was then pulled quickly down (towards the bottom) and backwards (towards, and then behind the observer), then out of the water column covering a path of 1 meter. Any larval amphibians captured were identified to species and counted, then released at the station.

Pipe Samplers. Three pipe samples were taken at each station approximately 3 meters apart to prevent disturbance. Pipe samplers were constructed from 30 cm diameter culvert pipe, 1 meter in height. Handles were attached near the top of the pipe sampler. Pipe samples were taken by projecting the pipe sampler roughly 1 meter in front of the observer (while hanging onto the handles), then pushing it forcibly straight down through the water column. Once the pipe sampler was situated, a 25.4 cm x 15.2 cm aquarium dip net was then used to sample larvae from within the tube. Dip nets were extended flush with the top of the substrate then, with a circular motion the dip net was moved to "sweep" the entire bottom of the sampler in a 360^0 rapid sweep; then quickly drawn up through the tube. After each dip net, any larvae captured were identified to species and counted. Dip net samples were taken repeatedly, until 5 consecutive sweeps yielded no larval amphibians. This method is similar to sampling used by Skelly (1992) in Michigan.

Funnel Traps. One plastic funnel trap was placed at each station. The funnel trap was a standard-sized, near cylindrical minnow trap, 43.2 cm long and 22.9 cm maximum diameter (at center of trap). Mesh size varied along the trap and ranged from 2 x 4 mm (at the 2 ends) to 4 x 7 mm (at the center). Dimensions of each funnel were: 15.5 cm wide, 11.4 cm deep, with a 2.4 cm diameter entrance hole. Rocks were placed in the trap to prevent it from floating. Traps were checked every 24 hours for 3 days. Any amphibian larvae captured were identified to species and counted.

Bottle Traps. One plastic bottle trap was placed at each station and checked every 24 hours for 3 days (same time as checking the funnel traps). A small rock was placed in the bottle to prevent it from floating. The bottle traps were constructed from two 2-litre plastic soda bottles. The tapered part of one bottle (top) was cut off and inverted and attached to the base of the bottle with clear plastic waterproof tape. The tapered part of a second bottle was also inverted to act as a funnel on the other end of the trap. The neck of each of the funnels was cut so that the opening was 2.4 cm and width and depth of the funnel was 10.5 cm and 6.5 cm, respectively. Small slits or holes were made in the trap to help keep the trap submerged. The bottle traps were similar to those used by Smith and Rettig (1996), Richter (1995), and Griffiths (1985), but had 2 funnel openings (instead of 1) and a larger entrance hole.

Data Analysis

Presence of a species as well as overall species richness at a site was determined by using the results of all sampling methods combined. Probability of capture of 4 common species: *Amybstoma maculatum* (spotted salamander), *Notophthalmus viridescens* (eastern newt), *Rana clamitans* (green frog), and *Rana catesbeiana* (bull frog) was determined for each of the 4 techniques. For each site at which a species was documented, the proportion of stations that the species was recorded was calculated for each technique. For example, imagine that spotted salamanders were documented at site A and site A had 20 stations. If spotted salamanders had been recorded at 10 stations using dip nets, 5 using pipe samplers, and 0 using funnel traps and bottle traps, then the proportion of stations would be: $p = 0.50$ for dip nets, $p = 0.25$ for pipe samplers, and $p = 0.00$ for both funnel and bottle traps. For the 4 common species, I averaged the proportion of stations at which the species was detected for each technique across all sites at which the species was recorded. The mean value and standard error were then used to determine a binomial distribution indicating the probability of detection of a species per unit of effort (i.e., number of stations) for each technique, as well as the standard error of that distribution. Based on this analysis, I determined the minimum number of stations required to

document the presence of each of the 4 common species, with a probability of 90%, given that the species is actually present.

I calculated the amount of time to implement a technique by averaging the number of person hours per station across all sites for each of the techniques; this was done for the number of sampling stations used for a typical medium and large wetland: 12 and 24, respectively. Similarly, I calculated the mean species richness for a medium and large wetland, given that the 4 key species were present, for each of the techniques. I also calculated the mean numbers of individuals of a given species captured per station for each technique, averaged across all sites in which they were documented.

RESULTS

Green frog larvae were documented at all 30 sites; eastern newt at 26 sites; spotted salamander at 22 sites; and bull frog at 7 sites (Appendix A). Spring peeper (*Pseudacris crucifer*) and pickerel frog (*Rana palustris*) larvae were captured at 6 and 12 sites, respectively; these 2 species were not analyzed further because they were captured in low numbers and many larvae had already reached metamorphosis prior to sampling. When considering all sampling techniques combined, overall species richness of the sites ranged from 1 – 5.

For all 4 focal species (i.e., spotted salamanders, eastern newts, green frogs, and bull frogs), funnel traps had the highest probability of detection for a given level of effort (i.e., number of stations) (Figures 3.1 – 3.4; Table 3.1). For spotted salamanders and bull frogs, dip nets were the least effective; for eastern newts, bottle traps performed the poorest; and for green frogs, pipe samplers and bottle traps had the lowest probability of detection for a given level of effort. Green frog larvae had the highest probability of detection and spotted salamanders had the lowest for all 4 techniques. Minimum number of stations required to detect the presence of each species of amphibian larvae showed similar relative differences between the species and techniques as for overall probability of detection (Table 3.2).

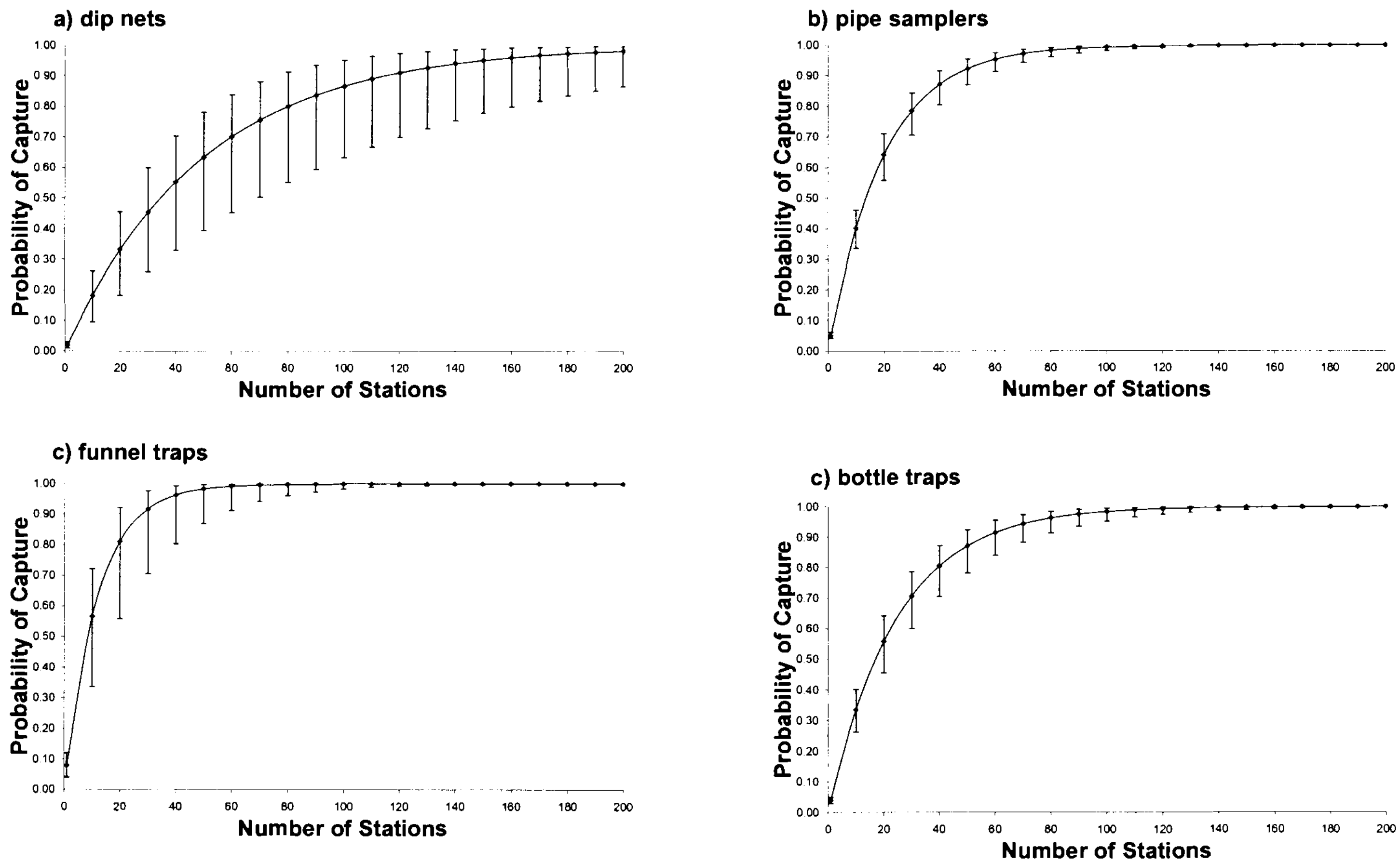

Figure 3.1. Probability of capture of *Ambystoma maculatum* larvae (mean + standard error) per number of sampling stations for 4 sampling techqniques in wetlands (n = 22).

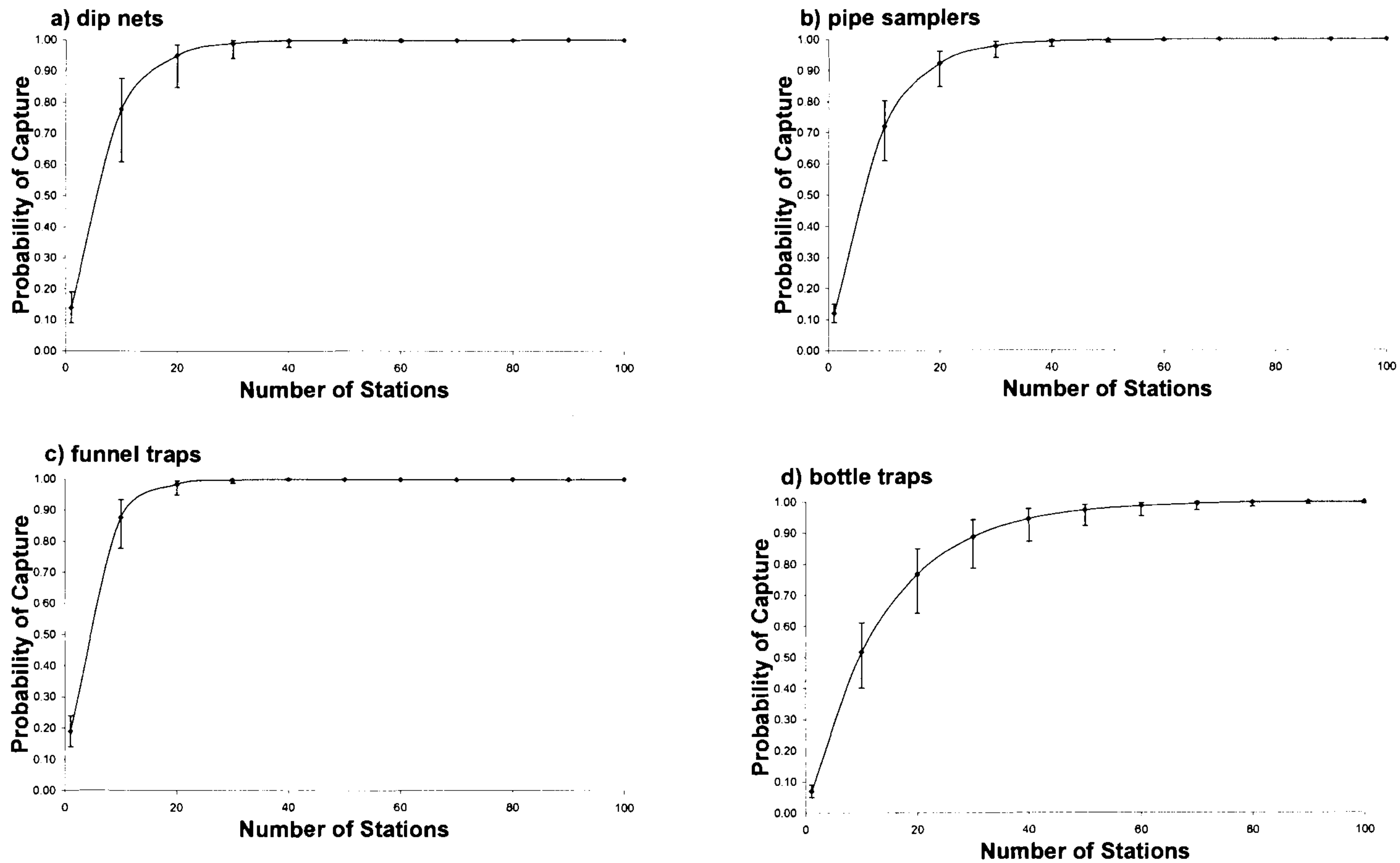

Figure 3.2. Probability of capture of *Notophthalmus viridescens* larvae (mean + standard error) per number of sampling stations for 4 sampling techqniques in wetlands (n = 26).

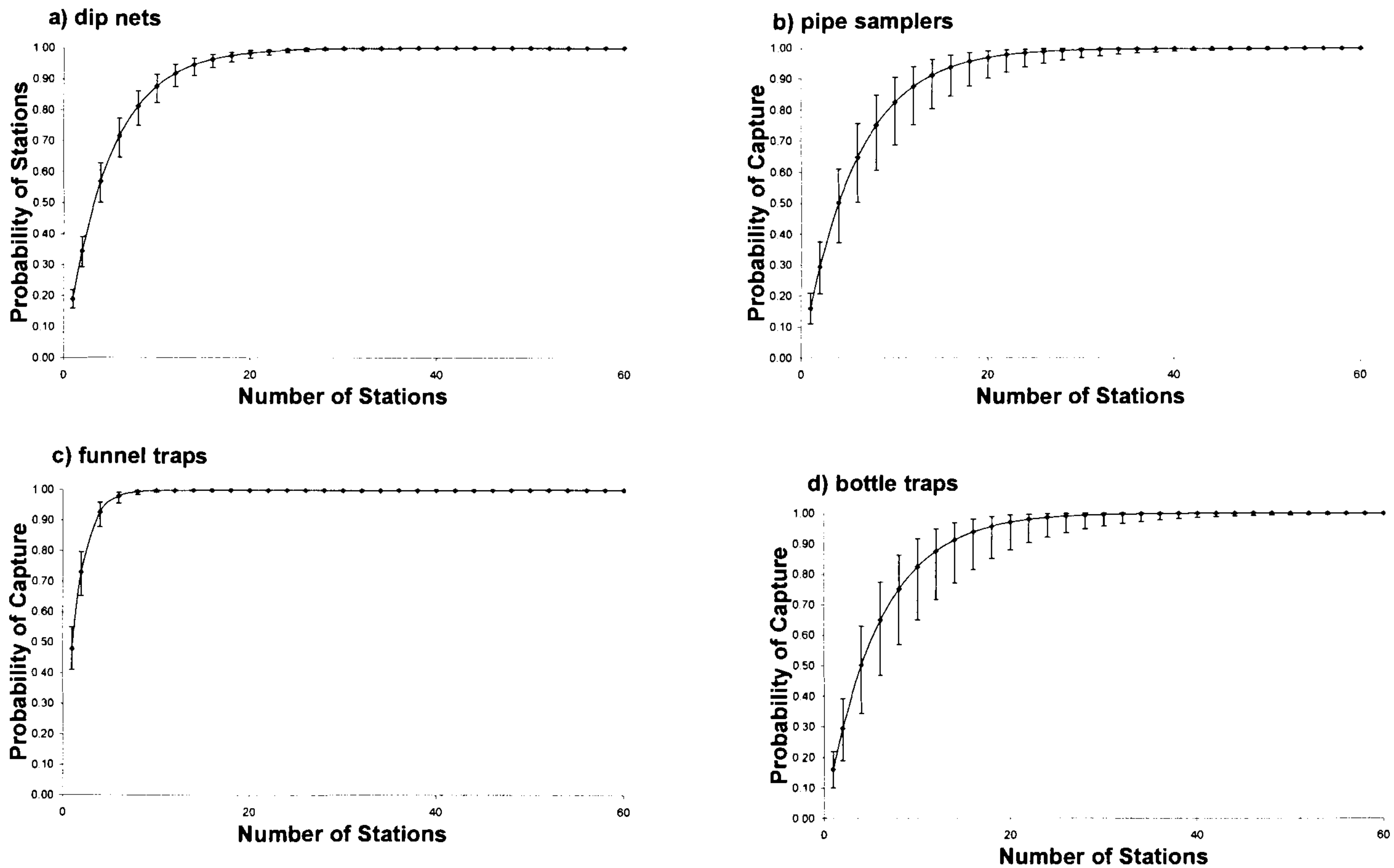

Figure 3.3. Probability of capture of *Rana clamitans* larvae (mean + standard error) per number of sampling stations for 4 sampling techqniques in wetlands (n = 30).

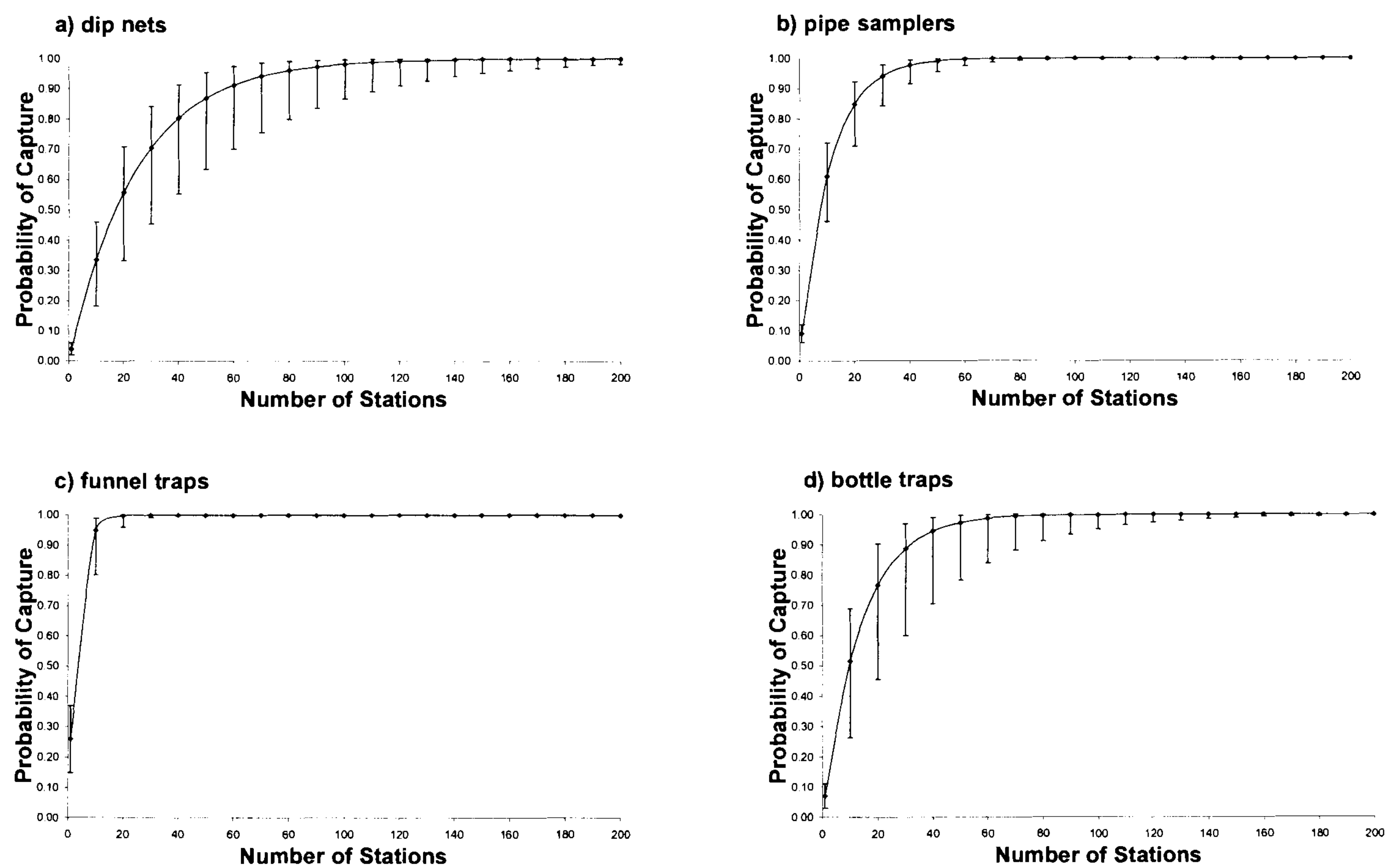

Figure 3.4. Probability of capture of *Rana catesbeiana* larvae (mean + standard error) per number of sampling stations for 4 sampling techqniques in wetlands (n = 7).

Table 3.1. Proportion of stations (mean ± standard error) at which each species of amphibian larvae was detected for all sites at which the species was recorded, for each of 4 sampling techniques.

	DIP NET	PIPE SAMPLER	FUNNEL TRAP	BOTTLE TRAP
Ambystoma maculatum (n = 22)	0.02 ± 0.01	0.05 ± 0.01	0.08 ± 0.04	0.04 ± 0.01
Notophthalmus viridescens (n = 26)	0.14 ± 0.05	0.12 ± 0.03	0.19 ± 0.05	0.07 ± 0.02
Rana clamitans (n = 30)	0.19 ± 0.03	0.16 ± 0.05	0.48 ± 0.07	0.16 ± 0.06
Rana catesbeiana (n = 7)	0.04 ± 0.02	0.09 ± 0.03	0.26 ± 0.11	0.07 ± 0.04

Table 3.2. Minimum number of stations required to detect each species of amphibian larvae for each of 4 sampling techniques, based on sampling in 30 wetlands in Acadia National Park, 1999.

	DIP NET	PIPE SAMPLER	FUNNEL TRAP	BOTTLE TRAP
Ambystoma maculatum (n = 22)	112	44	28	56
Notophthalmus viridescens (n = 26)	15	18	11	33
Rana clamitans (n = 30)	11	13	4	13
Rana catesbeiana (n = 7)	56	24	8	32

The mean estimate of number of person hours per station (averaged across all 30 sites) was lowest for dip nets and was similar for pipe samplers, funnel traps, and bottle traps (Table 3.3). Given the calculated probability of detection for each of the focal species and techniques, mean species richness was highest for funnel traps and lowest for dip nets (Table 3.4). In terms of numbers of individuals captured (Table 3.5), funnel traps generally captured the most spotted salamanders and bull frogs. For eastern newts, pipe samplers captured the most individuals whereas for green frogs, either pipe samplers or funnel traps typically captured the most individuals. Dip nets generally yielded the lowest numbers of individuals across species.

Cost of the equipment to implement each technique varied: one dip net (purchased from BIOEQUIP) was roughly $50.00; one pipe sampler (custom made at a local metalworking factory) was about $25.00; 1 plastic funnel (minnow) trap (purchased from Plasti-Lite Corporation; now available from Nylon Net Company) was $6.27; 1 plastic bottle trap cost approximately $0.50, plus labor for construction. Because number of sites sampled and number of funnel or bottle traps used will vary from study to study, cost of this equipment was not analyzed further.

DISCUSSION

The choice of a technique for sampling amphibian larvae will vary, depending on the particular question being asked. However, a few generalizations can be made. Funnel traps were consistently superior to the other methods tested in terms of probability of capture of the 4 focal species of larvae, as well as for determining species richness. Funnel traps also generally captured high numbers of individuals for each of the key species. The number of person hours required for sampling was similar for funnel traps, pipe samplers, and bottle traps; however, because it took 4 days to operate funnel traps (1 day for setting traps and 3 days of checking), travel time to and from study sites will be greater for these methods. I did not consider this issue in my calculations because it is site specific. Funnel traps are recommended as a sampling method for larval (and adult) amphibians in a variety of lentic habitats in the Pacific Northwest, particularly where visibility or maneuverability in the water column hinders other sampling

Table 3.3. Number of person hours (mean ± standard error) to sample at one station, a medium wetland (i.e., 12 sampling stations), and a large wetland (i.e., 24 sampling stations) for 4 larval sampling techniques.

	DIP NET	PIPE SAMPLER	FUNNEL TRAP	BOTTLE TRAP
Time for 1 station	0:12 ± 0:01	0:17 ± 0:01	0:17 ± 0:01	0:17 ± 0:01
Medium wetland (12 stations)	2:24 ± 0:12	3:24 ± 0:12	3:24 ± 0:12	3:24 ± 0:12
Large wetland (24 stations)	4:48 ± 0:24	6:48 ± 0:24	6:48 ± 0:24	6:48 ± 0:24

Table 3.4. Mean species richness of larval amphibians detected for a medium wetland (i.e., 12 sampling stations) and a large wetland (i.e., 24 sampling stations), given that *Ambystoma maculatum*, *Notophthalmus viridescens*, *Rana clamitans*, and *Rana catesbeiana* larvae are present and total species richness is 4, for 4 larval sampling techniques.

	DIP NET	PIPE SAMPLER	FUNNEL TRAP	BOTTLE TRAP
Medium wetland (12 stations)	2.37	2.80	3.52	2.43
Large wetland (24 stations)	2.96	3.54	3.85	3.24

Table 3.5. Number of amphibian larvae (mean ± standard error) captured per sampling station for a subset of 30 wetlands for which the particular species was recorded as present.

	DIP NET	PIPE SAMPLER	FUNNEL TRAP	BOTTLE TRAP
Ambystoma maculatum (n = 22)	0.28 ± 0.18	0.27 ± 0.11	0.70 ± 0.25	0.10 ± 0.04
Notophthalmus viridescens (n = 26)	0.42 ± 0.17	0.83 ± 0.51	0.44 ± 0.13	0.23 ± 0.11
Rana clamitans (n = 30)	0.70 ± 0.27	2.73 ± 0.99	2.68 ± 0.50	0.85 ± 0.32
Rana catesbeiana (n = 7)	0.03 ± 0.02	0.24 ± 0.13	0.42 ± 0.19	0.08 ± 0.04

methods (see Adams et al. 1997). In addition, because the skill and experience of the field worker has little impact on capture success, funnel trapping enables the development of trapping protocols that can be consistently repeated across sites (Adams et al. 1997).

Bottle traps typically yielded the lowest probability of capture for a given species as well as captured the fewest individuals (Figures 3.1 – 3.4, Tables 3.1 and 3.5), and, thus, their use is not supported by this study. In contrast, studies in the Pacific Northwest had favorable results with bottle traps of a slightly different design (Richter 1995). However, species assemblages differ between the regions; e.g., in the northeast, bull frog tadpoles take 2 years to develop and grow to such a large size that the entrance hole for Richter's bottle trap is too small for them.

Pipe samplers and dip nets performed similarly, although pipe samplers tended to have greater success in terms of both probability of capture as well as in abundance of individuals. However, the number of person hours per station was much lower for dip nets than for pipe samplers (as well as the other techniques) and, thus, for a given level of effort, more stations could be added using dip nets, thereby increasing the likelihood of detecting uncommon species.

In some situations, high numbers of individuals may be desired (e.g., sampling to document the presence or abundance of deformities). However, to generate reliable population estimates for a species at a given wetland, consistency of captures within and among stations would be necessary. In this study, overall consistency of captures within and between stations for all of the techniques was low. Specifically, most samples yielded no larval amphibians, presumably these wetlands were fairly large and had low densities of amphibian larvae. This suggests that some questions cannot be addressed with these methods. For example, density estimates or population indices will have high standard errors. However, it may be possible to use these techniques for other types of wetlands (e.g., woodland pools or smaller wetlands) if the likelihood of capture of individuals was greater.

In terms of overall performance, the use of funnel traps was best supported by this study. Pipe samplers and dip nets also showed promise. Because dip nets took less time to sample per station as compared to the other methods, number of samples taken could be increased to

increase numbers of captures without a substantial increase in effort. The use of bottle traps was not supported by this study.

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APPENDICES

Appendix A. Locations of study sites.

Table A.1. Approximate locations of study sites.

Site	UTM Easting	UTM Northing
18	556469	4913073
25	556327	4912735
28	556837	4912029
107	560067	4916731
113	559521	4916658
183	548278	4908687
184	548249	4908620
186	547679	4908630
194	549122	4906514
Aram's VP	565062	4910760
B19	557979	4913096
B75	560495	4914380
B99	560856	4916145
Becky's vp	559342	4916878
Beehive	564716	4909348
Bill's Winterberry vp	562177	4912818
Breakneck Pond	559331	4914883
Bruce's vp	560630	4914725
Bubble Middle	561103	4909220
Bubble North	560998	4909551
Bubble South	561118	4908875
C41	559519	4916378
Compass Harbor vp	561405	4915595
Duck Pond	549470	4907443

Table A.1 continued.

Site	UTM Easting	UTM Northing
Eagle Lake C.R.	559429	4913974
East of Fawn Pond	559106	4917031
East Otter Cliff Beaver	563973	4908935
East Otter Cliff vp	563950	4908852
Fawn Pond	558640	4917054
Gilley Beaver	551430	4904580
Gorge Trail Beaver	561975	4912780
Gorge Trail vp	562177	4912668
Halfmoon Pond	559639	4915319
HQVP	559106	4913043
HHH	557746	4912007
Hunter's Brook North	561900	4906749
Hunter's Brook South	562771	4905690
Lake Wood	558272	4917264
Leech	559504	4916934
Lifesaver	548319	4903183
Long Pond vp North	550477	4907555
Long Pond vp South	550482	4907525
MAC'S	556387	4912562
MB's Fav	558625	4912082
Mill Field Reservoir	550734	4904852
North of Halfmoon Pond	559519	4915507
North of Pinocchio	564153	4912375
North of Witch Hole	560653	4916581

Table A.1 continued.

Site	UTM Easting	UTM Northing
Northwestmost	558505	4912247
Nursery vp	565407	4909092
old B-23	557273	4911954
Otter vp	556522	4912517
Pinocchio	564198	4912112
Richardson Brook Beaver	556357	4912330
Round Pond	549769	4910803
Sand Beach	564987	4909122
Schooner Head vp	565174	4910557
Schooner Head Beaver	565107	4910459
Seal Cove Road vp	549413	4902709
Sieur de Mont vp	562948	4912617
South of The Tarn	563312	4910572
Southeast of The Bowl	564611	4908792
Southeastmost	558595	4911946
Southwestmost	558415	4912014
Steve's vp	561351	4915386
Stick Wetland	559721	4915657
Swallowtail	559413	4914177
The Bowl	564183	4909310
Top of the Hill Tarn	562831	4909809
West Otter Creek	562891	4909809
Western Mtn. Rd. North	548838	4903390
Western Mtn. Rd. South	548808	4903294

Appendix B. Data for decision tree analysis.

Table B.1. Number of wood frog and spotted salamander egg masses.

Site	# of Wood Frog egg masses (2000)	# of Wood Frog egg masses (2001)	# of Wood Frog egg masses (mean)	# of Spotted Salamander egg masses (2000)	# of Spotted Salamander egg masses (2001)	# of Spotted Salamander egg masses (mean)
18	14	13	14	72	70	71
25	20	21	21	20	10	15
28	9	0	5	7	0	4
107	2	2	2	154	82	118
113	0	0	0	41	37	39
183	0	0	0	15	15	15
184	0	0	0	45	35	40
186	20	22	21	94	11	53
194	0	0	0	17	3	10
Aram's VP	0	0	0	5	0	3
B19	0	0	0	11	28	20
B75	9	13	11	11	60	36
B99	0	0	0	1	13	7
Becky's vp	0	0	0	6	3	5
Beehive	6	2	4	71	59	65
Bill's Winterberry vp	0	11	6	8	1	5
Breakneck Pond	0	1	1	116	142	129
Bruce's vp	7	12	10	45	38	42
Bubble Middle	86	48	67	209	91	150
Bubble North	0	0	0	28	11	20
Bubble South	0	0	0	9	1	5
C41	6	2	4	117	107	112
Compass Harbor vp	0	0	0	97	26	62
Duck Pond	0	5	3	549	242	396
Eagle Lake C.R.	54	17	36	23	3	13
East of Fawn Pond	85	153	119	913	148	531
East Otter Cliff Beaver	30	44	37	31	37	34
East Otter Cliff vp	20	38	29	54	56	55
Fawn Pond	0	0	0	0	3	2
Gilley Beaver	0	1	1	126	54	90

Table B.1 continued.

Site	# of Wood Frog egg masses (2000)	# of Wood Frog egg masses (2001)	# of Wood Frog egg masses (mean)	# of Spotted Salamander egg masses (2000)	# of Spotted Salamander egg masses (2001)	# of Spotted Salamander egg masses (mean)
Gorge Trail Beaver	0	0	0	132	58	95
Gorge Trail vp	11	8	10	21	8	15
Halfmoon Pond	0	0	0	21	15	18
HQVP	48	83	66	206	229	218
HHH	40	34	37	307	191	249
Hunter's Brook North	1	0	1	47	6	27
Hunter's Brook South	1	0	1	84	34	59
Lake Wood	0	0	0	12	6	9
Leech	0	0	0	17	13	15
Lifesaver	0	0	0	171	36	104
Long Pond vp North	100	87	94	27	4	16
Long Pond vp South	45	46	46	43	15	29
MAC'S	0	0	0	93	59	76
MB's Fav	136	80	108	105	168	137
Mill Field Reservoir	0	0	0	91	6	49
North of Halfmoon Pond	0	0	0	33	26	30
North of Pinocchio	0	0	0	23	26	25
North of Witch Hole	1	2	2	248	426	337
Northwestmost	7	5	6	0	0	0
Nursery vp	23	25	24	237	47	142
old B-23	41	20	31	32	32	32
Otter vp	37	65	51	59	126	93
Pinocchio	0	0	0	0	37	19
Richardson Brook Beaver	0	0	0	47	39	43
Round Pond	0	0	0	62	13	38
Sand Beach	0	0	0	31	26	29
Schooner Head vp	4	4	4	22	11	17
Schooner Head Beaver	0	7	4	28	48	38
Seal Cove Road vp	91	60	76	75	28	52
Sieur de Mont vp	14	5	10	21	2	12

Table B.1 continued.

Site	# of Wood Frog egg masses (2000)	# of Wood Frog egg masses (2001)	# of Wood Frog egg masses (mean)	# of Spotted Salamander egg masses (2000)	# of Spotted Salamander egg masses (2001)	# of Spotted Salamander egg masses (mean)
South of The Tarn	2	1	2	56	37	47
Southeast of The Bowl	18	17	18	156	216	186
Southeastmost	0	0	0	9	9	9
Southwestmost	0	0	0	65	13	39
Steve's vp	8	6	7	33	53	43
Stick Wetland	0	0	0	8	1	5
Swallowtail	4	1	3	70	7	39
The Bowl	0	0	0	0	0	0
Top of the Hill Tarn	22	22	22	37	75	56
West Otter Creek	0	0	0	31	13	22
Western Mtn. Rd. North	48	114	81	177	9	93
Western Mtn. Rd. South	7	5	6	7	4	6

Table B.2. Categories of wood frog and spotted salamander egg masses.

Site	Wood Frog Category (2000)	Wood Frog Category (2001)	Wood Frog Category (mean)	Spotted Salamander Cateogory (2000)	Spotted Salamander Cateogory (2001)	Spotted Salamander Cateogory (mean)
18	medium	medium	medium	medium	medium	medium
25	medium	medium	medium	low	low	low
28	low	low	low	low	low	low
107	low	low	low	high	medium	high
113	low	low	low	low	low	low
183	low	low	low	low	low	low
184	low	low	low	low	low	low
186	medium	medium	medium	medium	low	low
194	low	low	low	low	low	low
Aram's VP	low	low	low	low	low	low
B19	low	low	low	low	low	low
B75	low	medium	medium	low	medium	low
B99	low	low	low	low	low	low
Becky's vp	low	low	low	low	low	low
Beehive	low	low	low	medium	medium	medium
Bill's Winterberry vp	low	medium	low	low	low	low
Breakneck Pond	low	low	low	high	high	high
Bruce's vp	low	medium	medium	low	low	low
Bubble Middle	high	high	high	high	medium	high
Bubble North	low	low	low	low	low	low
Bubble South	low	low	low	low	low	low
C41	low	low	low	high	medium	high
Compass Harbor vp	low	low	low	medium	low	medium
Duck Pond	low	low	low	high	high	high
Eagle Lake C.R.	high	medium	medium	low	low	low
East of Fawn Pond	high	high	high	high	high	high
East Otter Cliff Beaver	medium	high	medium	low	low	low
East Otter Cliff vp	medium	medium	medium	low	medium	medium
Fawn Pond	low	low	low	low	low	low
Gilley Beaver	low	low	low	high	low	medium

Table B.2 continued.

Site	Wood Frog Category (2000)	Wood Frog Category (2001)	Wood Frog Category (mean)	Spotted Salamander Cateogory (2000)	Spotted Salamander Cateogory (2001)	Spotted Salamander Cateogory (mean)
Gorge Trail Beaver	low	low	low	high	medium	medium
Gorge Trail vp	medium	low	medium	low	low	low
Halfmoon Pond	low	low	low	low	low	low
HQVP	high	high	high	high	high	high
HHH	high	medium	medium	high	high	high
Hunter's Brook North	low	low	low	low	low	low
Hunter's Brook South	low	low	low	medium	low	medium
Lake Wood	low	low	low	low	low	low
Leech	low	low	low	low	low	low
Lifesaver	low	low	low	high	low	medium
Long Pond vp North	high	high	high	low	low	low
Long Pond vp South	high	high	high	low	low	low
MAC'S	low	low	low	medium	medium	medium
MB's Fav	high	high	high	medium	high	high
Mill Field Reservoir	low	low	low	medium	low	low
North of Halfmoon Pond	low	low	low	low	low	low
North of Pinocchio	low	low	low	low	low	low
North of Witch Hole	low	low	low	high	high	high
Northwestmost	low	low	low	low	low	low
Nursery vp	medium	medium	medium	high	low	high
old B-23	high	medium	medium	low	low	low
Otter vp	medium	high	high	medium	high	medium
Pinocchio	low	low	low	low	low	low
Richardson Brook Beaver	low	low	low	low	low	low
Round Pond	low	low	low	medium	low	low
Sand Beach	low	low	low	low	low	low
Schooner Head vp	low	low	low	low	low	low
Schooner Head Beaver	low	low	low	low	low	low
Seal Cove Road vp	high	high	high	medium	low	low
Sieur de Mont vp	medium	low	medium	low	low	low

Table B.2 continued.

Site	Wood Frog Category (2000)	Wood Frog Category (2001)	Wood Frog Category (mean)	Spotted Salamander Cateogory (2000)	Spotted Salamander Cateogory (2001)	Spotted Salamander Cateogory (mean)
South of The Tarn	low	low	low	medium	low	low
Southeast of The Bowl	medium	medium	medium	high	high	high
Southeastmost	low	low	low	low	low	low
Southwestmost	low	low	low	medium	low	low
Steve's vp	low	low	low	low	low	low
Stick Wetland	low	low	low	low	low	low
Swallowtail	low	low	low	medium	low	low
The Bowl	low	low	low	low	low	low
Top of the Hill Tarn	medium	medium	medium	low	medium	medium
West Otter Creek	low	low	low	low	low	low
Western Mtn. Rd. North	high	high	high	high	low	medium
Western Mtn. Rd. South	low	low	low	low	low	low

Table B.3. Pool characteristics I. (Present = 1; Absent = 0)

Site	Area (m^2)	Perimeter (m)	Maximum Depth (cm)	Perimeter : Maximum Depth	Inlet Present	Outlet Present
18	148.78	59	46.5	1.3	1	1
25	1144.32	151	42.0	3.6	0	1
28	761.09	101	43	2.3	0	0
107	4658.47	346	71.0	4.9	0	1
113	1113.81	134	75.0	1.8	1	1
183	116.61	43	99.0	0.4	0	0
184	732.41	104	163.0	0.6	0	0
186	1276.75	140	41.0	3.4	0	0
194	273.97	85	77.0	1.1	1	1
Aram's VP	465.22	86	66.0	1.3	0	0
B19	1199.25	136	132	1.0	1	1
B75	14072.80	467	95.0	4.9	1	1
B99	7110.03	396	130	3.0	1	1
Becky's vp	337.80	104	44	2.4	0	0
Beehive	7221.78	358	75.0	4.8	0	1
Bill's Winterberry vp	892.91	113	37	3.0	0	0
Breakneck Pond	45063.00	1065	200	5.3	1	1
Bruce's vp	547.41	144	83	1.7	0	0
Bubble Middle	3237.14	315	53.5	5.9	1	1
Bubble North	4158.81	246	72.0	3.4	1	1
Bubble South	1371.16	138	66.0	2.1	1	1
C41	1489.13	200	101.5	2.0	1	1
Compass Harbor vp	165.55	55	65.0	0.8	0	0
Duck Pond	6918.30	546	200	2.7	0	1
Eagle Lake C.R.	3131.16	249	75	3.3	0	1
East of Fawn Pond	29688.00	1046	200	5.2	0	1
East Otter Cliff Beaver	1868.31	207	165.0	1.3	1	1
East Otter Cliff vp	1562.12	184	42.0	4.4	0	0
Fawn Pond	19789.60	630	200	3.2	0	1
Gilley Beaver	357.75	70	66	1.1	1	1

Table B.3 continued.

Site	Area (m^2)	Perimeter (m)	Maximum Depth (cm)	Perimeter : Maximum Depth	Inlet Present	Outlet Present
Gorge Trail Beaver	599.73	114	101.0	1.1	1	1
Gorge Trail vp	521.31	85	110.0	0.8	0	0
Halfmoon Pond	20440.40	545	200	2.7	0	1
HQVP	1118.02	182	74.0	2.5	0	0
HHH	466.01	108	88.0	1.2	1	1
Hunter's Brook North	3409.13	230	111	2.1	1	1
Hunter's Brook South	32585.60	1266	70	18.1	1	0
Lake Wood	84240.60	2071	200	10.4	1	1
Leech	35708.80	987	200	4.9	1	1
Lifesaver	4348.13	273	90.0	3.0	0	1
Long Pond vp North	614.36	103	47.0	2.2	0	0
Long Pond vp South	343.71	75	76.5	1.0	0	0
MAC'S	13268.40	551	150.0	3.7	1	1
MB's Fav	4558.37	297	114.0	2.6	0	1
Mill Field Reservoir	858.38	117	206.0	0.6	1	1
North of Halfmoon Pond	1052.88	124	98	1.3	1	1
North of Pinocchio	6143.84	466	200.0	2.3	1	1
North of Witch Hole	15816.46	656	132.0	5.0	0	1
Northwestmost	3520.25	266	35.0	7.6	0	0
Nursery vp	1288.78	146	74.0	2.0	0	0
old B-23	2260.63	261	45	5.8	1	1
Otter vp	1019.78	147	90.5	1.6	0	0
Pinocchio	53582.90	919	200.0	4.6	1	1
Richardson Brook Beaver	35904.56	253	150	1.7	1	1
Round Pond	154267.00	2343	200	11.7	1	1
Sand Beach	6480.70	572	150.0	3.8	1	1
Schooner Head vp	427.61	124	48.0	2.6	0	0
Schooner Head Beaver	11293.10	536	124.0	4.3	1	1
Seal Cove Road vp	379.23	78	71.5	1.1	0	0
Sieur de Mont vp	219.36	61	65.0	0.9	0	0

Table B.3 continued.

Site	Area (m^2)	Perimeter (m)	Maximum Depth (cm)	Perimeter : Maximum Depth	Inlet Present	Outlet Present
South of The Tarn	5680.31	438	95.0	4.6	0	1
Southeast of The Bowl	6441.57	367	137.0	2.7	1	1
Southeastmost	537.50	96	52	1.9	0	1
Southwestmost	1365.63	141	94	1.5	1	1
Steve's vp	472.80	118	44.0	2.7	0	0
Stick Wetland	19797.80	585	150	3.9	1	1
Swallowtail	9334.94	445	95	4.7	1	1
The Bowl	47698.10	959	200.0	4.8	1	1
Top of the Hill Tarn	8616.45	423	146.5	2.9	1	1
West Otter Creek	6745.75	396	92.0	4.3	1	1
Western Mtn. Rd. North	1030.91	174	57.0	3.1	0	0
Western Mtn. Rd. South	408.00	86	50.0	1.7	0	0

Table B.4. Pool characteristics II. (Hydroperiod Category: 1 = shortest; 7 = longest)

(Present = 1; Absent = 0)

Site	Site Type	Hydroperiod Cateogory	Unfrozen Water Present in Winter?	Index of Primary Productivity (g)
18	connected-small	4	0	0.25
25	connected-small	1	0	0.04
28	upland-isolated	1		
107	connected-small	5		
113	connected-small	5		
183	upland-isolated	6		
184	upland-isolated	6		
186	upland-isolated	1		
194	connected-small	2		
Aram's VP	upland-isolated	4		
B19	connected-small	7		
B75	connected-large	5		
B99	connected-small	5		
Becky's vp	upland-isolated	2		
Beehive	connected-small	5	1	0.11
Bill's Winterberry vp	upland-isolated	3		
Breakneck Pond	connected-large	7		
Bruce's vp	upland-isolated	5		
Bubble Middle	connected-small	4	0	0.11
Bubble North	connected-small	6		
Bubble South	connected-small	5		
C41	connected-small	6	1	0.25
Compass Harbor vp	upland-isolated	3		
Duck Pond	connected-small	7		
Eagle Lake C.R.	connected-small	4		
East of Fawn Pond	connected-large	6		
East Otter Cliff Beaver	connected-small	5	1	0.09
East Otter Cliff vp	upland-isolated	3	0	0.11
Fawn Pond	connected-large	7		
Gilley Beaver	connected-small	5		

Table B.4 continued.

Site	Site Type	Hydroperiod Cateogory	Unfrozen Water Present in Winter?	Index of Primary Productivity (g)
Gorge Trail Beaver	connected-small	6	1	0.08
Gorge Trail vp	upland-isolated	1		
Halfmoon Pond	connected-large	7		
HQVP	upland-isolated	1	0	0.11
HHH	connected-large	6	1	0.12
Hunter's Brook North	connected-small	6		
Hunter's Brook South	connected-large	6		
Lake Wood	connected-large	7		
Leech	connected-large	7		
Lifesaver	connected-small	6		
Long Pond vp North	upland-isolated	2	0	0.01
Long Pond vp South	upland-isolated	2	0	0.05
MAC'S	connected-large	7	1	0.16
MB's Fav	connected-small	3	0	0.04
Mill Field Reservoir	connected-small	7		
North of Halfmoon Pond	connected-small	5		
North of Pinocchio	connected-small	7		
North of Witch Hole	connected-large	7	1	0.31
Northwestmost	upland-isolated	3		
Nursery vp	upland-isolated	4		
old B-23	connected-small	4		
Otter vp	upland-isolated	3	1	0.13
Pinocchio	connected-large	7		
Richardson Brook Beaver	connected-large	7		
Round Pond	connected-large	7		
Sand Beach	connected-small	7		
Schooner Head vp	upland-isolated	3		
Schooner Head Beaver	connected-large	5		
Seal Cove Road vp	upland-isolated	1	0	0.04
Sieur de Mont vp	upland-isolated	4		

Table B.4 continued.

Site	Site Type	Hydroperiod Cateogory	Unfrozen Water Present in Winter?	Index of Primary Productivity (g)
South of The Tarn	connected-large	7	1	0.13
Southeast of The Bowl	connected-small	4	1	0.06
Southeastmost	connected-small	3		
Southwestmost	connected-small	5		
Steve's vp	upland-isolated	2	0	0.16
Stick Wetland	connected-large	7		
Swallowtail	connected-small	5		
The Bowl	connected-large	7		
Top of the Hill Tarn	connected-large	5	1	0.13
West Otter Creek	connected-small	6		
Western Mtn. Rd. North	upland-isolated	4		
Western Mtn. Rd. South	upland-isolated	1		

Table B.5. Landscape characteristics.

Site	Slope position	Percent Slope	Catchment Area (ha)	% of area within 1000 m covered by wetland
18	upper	3.33	22.28	9.86
25	mid	5.00	4.05	9.19
28	upper	2.85	2.03	7.55
107	mid	5.00	20.25	13.15
113	mid	7.50	85.05	13.37
183	upper	6.67	4.05	8.69
184	upper	0.05	2.03	9.54
186	lower/flat	6.67	12.15	5.57
194	mid	8.42	137.70	4.81
Aram's VP	lower/flat	3.96	12.15	1.54
B19	lower/flat	0.05	558.90	17.22
B75	mid	1.97	615.60	20.75
B99	lower/flat	3.24	137.70	12.24
Becky's vp	lower/flat	14.28	20.25	10.86
Beehive	mid	14.00	46.58	8.67
Bill's Winterberry vp	mid	13.18	16.20	11.36
Breakneck Pond	lower/flat	0.40	643.95	11.24
Bruce's vp	lower/flat	0.05	18.23	16.43
Bubble Middle	lower/flat	0.05	32.40	0.90
Bubble North	lower/flat	3.07	178.20	5.12
Bubble South	lower/flat	3.00	198.45	1.54
C41	mid	5.00	54.68	10.69
Compass Harbor vp	lower/flat	3.16	36.45	0.58
Duck Pond	mid	3.10	170.10	5.78
Eagle Lake C.R.	lower/flat	3.06	24.30	23.08
East of Fawn Pond	upper	1.97	81.00	10.04
East Otter Cliff Beaver	mid	10.00	170.10	4.91
East Otter Cliff vp	mid	10.00	10.13	4.66
Fawn Pond	mid	7.34	93.15	9.99
Gilley Beaver	lower/flat	5.42	141.75	7.33

Table B.5 continued.

Site	Slope position	Percent Slope	Catchment Area (ha)	% of area within 1000 m covered by wetland
Gorge Trail Beaver	mid	10.66	62.78	6.44
Gorge Trail vp	mid	14.29	8.10	11.82
Halfmoon Pond	mid	5.63	101.25	15.25
HQVP	upper	8.00	6.08	6.88
HHH	lower/flat	2.50	93.15	11.47
Hunter's Brook North	lower/flat	1.31	1385.10	1.60
Hunter's Brook South	lower/flat	0.73	307.80	1.71
Lake Wood	lower/flat	1.47	648.00	15.18
Leech	lower/flat	0.81	352.35	11.43
Lifesaver	mid	3.64	32.40	11.03
Long Pond vp North	lower/flat	2.00	12.15	1.22
Long Pond vp South	lower/flat	2.00	8.10	0.86
MAC'S	lower/flat	1.66	129.60	8.36
MB's Fav	upper	2.22	44.55	11.37
Mill Field Reservoir	lower/flat	5.63	328.05	0.66
North of Halfmoon Pond	mid	6.25	117.45	13.19
North of Pinocchio	mid	1.31	364.50	6.68
North of Witch Hole	lower/flat	0.05	26.33	5.79
Northwestmost	upper	0.05	4.05	19.78
Nursery vp	lower/flat	0.05	4.05	8.41
old B-23	mid	6.42	76.95	10.85
Otter vp	mid	7.50	8.10	7.47
Pinocchio	mid	1.89	275.40	8.13
Richardson Brook Beaver	lower/flat	2.74	194.40	9.27
Round Pond	lower/flat	0.59	384.75	30.72
Sand Beach	lower/flat	4.62	109.35	9.07
Schooner Head vp	mid	12.77	4.05	8.18
Schooner Head Beaver	lower/flat	1.68	109.35	8.38
Seal Cove Road vp	lower/flat	0.05	8.10	7.45
Sieur de Mont vp	lower/flat	7.31	16.20	16.53

Table B.5 continued.

Site	Slope position	Percent Slope	Catchment Area (ha)	% of area within 1000 m covered by wetland
South of The Tarn	lower/flat	0.05	74.93	4.49
Southeast of The Bowl	mid	10.00	64.80	5.74
Southeastmost	mid	5.88	20.25	18.74
Southwestmost	mid	1.79	76.95	15.61
Steve's vp	mid	10.00	20.25	6.50
Stick Wetland	lower/flat	1.88	194.40	17.51
Swallowtail	lower/flat	4.10	113.40	19.68
The Bowl	upper	6.33	89.10	8.35
Top of the Hill Tarn	mid	11.11	74.93	5.81
West Otter Creek	lower/flat	1.98	1296.00	6.33
Western Mtn. Rd. North	upper	6.66	4.05	11.87
Western Mtn. Rd. South	upper	5.82	4.05	10.70

Appendix C. Data for larval sampling in 1999.

Table C.1. Number of stations that each species of larval amphibian was captured at during dipnet sampling in 30 ponds in Acadia National Park, 1999. Total number of individuals captured is indicated in parentheses.

Site	Date Sampled (month/day/year)	Number of Stations	*Ambystoma maculatum*	*Notophthalmus viridescens*	*Pseudacris crucifer*	*Rana palustris*	*Rana clamitans*	*Rana catesbeiana*
B75	7/28/99	2	2 (8)	1 (8)	0 (0)	0 (0)	1 (1)	0 (0)
B99	7/28/99	2	0 (0)	0 (0)	0 (0)	0 (0)	1 (5)	0 (0)
Breakneck Pond	7/22/99	24	2 (3)	1 (1)	0 (0)	0 (0)	3 (3)	1 (1)
Bruce's vp	7/17/99	5	1 (5)	1 (1)	0 (0)	0 (0)	1 (1)	0 (0)
C41	7/29/99	4	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
107	7/28/99	1	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
113	7/29/99	2	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
183	8/5/99	1	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Duck Pond	8/10/99	8	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)
East of Fawn Pond	7/18/99	20	1 (1)	1 (1)	1 (4)	0 (0)	5 (9)	0 (0)
18	7/23/99	1	0 (0)	0 (0)	0 (0)	0 (0)	1 (8)	0 (0)
Fawn Pond	8/5/99	18	0 (0)	0 (0)	0 (0)	0 (0)	4 (4)	2 (2)
Gilley Beaver	8/10/99	1	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Gorge Trail Beaver	7/16/99	5	0 (0)	1 (2)	1 (1)	0 (0)	1 (1)	0 (0)
Halfmoon Pond	7/29/99	12	0 (0)	1 (2)	0 (0)	0 (0)	0 (0)	0 (0)
HHH	8/5/99	1	0 (0)	1 (2)	0 (0)	0 (0)	1 (1)	0 (0)
Hunter's Brook South	8/5/99	22	0 (0)	4 (4)	0 (0)	0 (0)	6 (20)	0 (0)
Leech	7/17/99	24	0 (0)	2 (2)	0 (0)	0 (0)	9 (19)	2 (2)

Table C1 continued.

Site	Date Sampled (month/day/year)	Number of Stations	*Ambystoma maculatum*	*Notophthalmus viridescens*	*Pseudacris crucifer*	*Rana palustris*	*Rana clamitans*	*Rana catesbeiana*
Lifesaver	8/4/99	6	0 (0)	0 (0)	0 (0)	0 (0)	1 (8)	0 (0)
Mac's	7/23/99	17	0 (0)	1 (1)	0 (0)	0 (0)	2 (2)	0 (0)
North of Pinnochio	8/3/99	14	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)
North of Witch Hole Pond	7/28/99	11	0 (0)	1 (1)	0 (0)	0 (0)	1 (1)	0 (0)
Pinnochio	8/3/99	11	0 (0)	1 (2)	0 (0)	0 (0)	0 (0)	0 (0)
Richardson Brook Beaver	7/23/99	12	0 (0)	3 (3)	0 (0)	1 (1)	2 (3)	0 (0)
Richardson Brook UB	7/23/99	5	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Schooner Head Road Beaver	8/3/99	2	0 (0)	1 (3)	0 (0)	0 (0)	1 (3)	0 (0)
South of The Tarn	8/4/99	15	0 (0)	6 (13)	0 (0)	1 (1)	4 (16)	0 (0)
Stick Wetland	7/29/99	16	1 (1)	8 (12)	0 (0)	0 (0)	2 (2)	0 (0)
Swallowtail	7/22/99	12	0 (0)	1 (1)	0 (0)	0 (0)	3 (3)	0 (0)
Top of the Hill Tarn	8/4/99	7	1 (1)	0 (0)	0 (0)	0 (0)	3 (8)	0 (0)

Table C.2. Number of stations that each species of larval amphibian was captured at during pipe sampling in 30 ponds in Acadia National Park, 1999. Total number of individuals captured is indicated in parentheses.

Site	Date Sampled (month/day/year)	Number of Stations	*Ambystoma maculatum*	*Notophthalmus viridescens*	*Pseudacris crucifer*	*Rana palustris*	*Rana clamitans*	*Rana catesbeiana*
B75	7/29/99	2	1 (4)	2 (26)	0 (0)	0 (0)	1 (1)	0 (0)
B99	7/29/99	2	0 (0)	0 (0)	0 (0)	0 (0)	2 (13)	0 (0)
Breakneck Pond	7/23/99	24	3 (4)	2 (5)	0 (0)	0 (0)	1 (1)	2 (2)
Bruce's vp	7/16/99	5	4 (5)	2 (3)	0 (0)	0 (0)	3 (7)	0 (0)
C41	7/28/99	4	2 (3)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
107	7/29/99	1	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
113	7/28/99	2	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
183	8/10/99	1	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Duck Pond	8/5/99	8	0 (0)	0 (0)	0 (0)	0 (0)	6 (14)	0 (0)
East of Fawn Pond	7/17/99	20	2 (2)	0 (0)	0 (0)	0 (0)	6 (89)	0 (0)
18	7/22/99	1	0 (0)	0 (0)	0 (0)	0 (0)	1 (10)	0 (0)
Fawn Pond	8/10/99	18	1 (1)	1 (1)	0 (0)	0 (0)	0 (0)	4 (11)
Gilley Beaver	8/5/99	1	0 (0)	1 (1)	0 (0)	0 (0)	1 (9)	0 (0)
Gorge Trail Beaver	7/17/99	5	0 (0)	1 (1)	1 (1)	0 (0)	2 (6)	0 (0)
Halfmoon Pond	7/28/99	12	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
HHH	8/10/99	1	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Hunter's Brook South	8/10/99	22	0 (0)	5 (10)	0 (0)	0 (0)	13 (58)	0 (0)
Leech	7/16/99	24	0 (0)	1 (3)	0 (0)	0 (0)	5 (18)	3 (20)

Table C.2 continued.

Site	Date Sampled (month/day/year)	Number of Stations	*Ambystoma maculatum*	*Notophthalmus viridescens*	*Pseudacris crucifer*	*Rana palustris*	*Rana clamitans*	*Rana catesbeiana*
Lifesaver	8/3/99	6	0 (0)	1 (1)	0 (0)	0 (0)	5 (18)	0 (0)
Mac's	7/22/99	17	1 (1)	2 (2)	0 (0)	0 (0)	2 (3)	0 (0)
North of Pinnochio	8/4/99	14	0 (0)	2 (2)	0 (0)	0 (0)	2 (13)	0 (0)
North of Witch Hole Pond	7/29/99	11	2 (3)	1 (1)	0 (0)	0 (0)	5 (11)	0 (0)
Pinnochio	8/4/99	11	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Richardson Brook Beaver	7/22/99	12	0 (0)	2 (2)	0 (0)	0 (0)	2 (15)	0 (0)
Richardson Brook UB	7/22/99	5	3 (7)	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)
Schooner Head Road Beaver	8/4/99	2	0 (0)	2 (8)	0 (0)	0 (0)	2 (10)	0 (0)
South of The Tarn	8/3/99	15	1 (1)	4 (8)	0 (0)	0 (0)	2 (37)	0 (0)
Stick Wetland	7/28/99	16	1 (1)	3 (8)	0 (0)	1 (1)	3 (31)	2 (2)
Swallowtail	7/23/99	12	1 (1)	2 (2)	0 (0)	0 (0)	0 (0)	0 (0)
Top of the Hill Tarn	8/3/99	7	0 (0)	0 (0)	0 (0)	1 (1)	4 (194)	0 (0)

Table C.3. Number of stations that each species of larval amphibian was captured at during funnel trap sampling in 30 ponds in Acadia National Park, 1999. Total number of individuals captured is indicated in parentheses.

Site	Date Sampled (month/day/year)	Number of Stations	*Ambystoma maculatum*	*Notophthalmus viridescens*	*Pseudacris crucifer*	*Rana palustris*	*Rana clamitans*	*Rana catesbeiana*
B75	7/24 – 7/27/99	2	2 (5)	1 (1)	0 (0)	0 (0)	2 (5)	0 (0)
B99	7/24 – 7/27/99	2	1 (1)	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)
Breakneck Pond	7/18 – 7/21/99	24	2 (3)	2 (2)	0 (0)	0 (0)	7 (12)	7 (10)
Bruce's vp	7/12 – 7/15/99	5	3 (10)	0 (0)	2 (2)	0 (0)	4 (7)	0 (0)
C41	7/24 – 7/27/99	4	3 (5)	1 (1)	0 (0)	0 (0)	3 (8)	0 (0)
107	7/24 – 7/27/99	1	1 (5)	0 (0)	0 (0)	0 (0)	1 (5)	0 (0)
113	7/24 – 7/27/99	2	0 (0)	1 (1)	0 (0)	0 (0)	1 (1)	0 (0)
183	8/6 – 8/9/99	1	0 (0)	0 (0)	0 (0)	0 (0)	1 (9)	0 (0)
Duck Pond	8/6 – 8/9/99	8	4 (5)	1 (1)	0 (0)	0 (0)	8 (25)	0 (0)
East of Fawn Pond	7/13 – 7/16/99	20	9 (19)	0 (0)	3 (7)	0 (0)	15 (38)	0 (0)
18	7/18 – 7/21/99	1	0 (0)	0 (0)	1 (1)	0 (0)	1 (8)	0 (0)
Fawn Pond	8/6 – 8/9/99	18	0 (0)	2 (2)	0 (0)	1 (1)	2 (3)	13 (25)
Gilley Beaver	8/6 – 8/9/99	1	0 (0)	1 (3)	0 (0)	0 (0)	1 (2)	0 (0)
Gorge Trail Beaver	7/12 – 7/15/99	5	0 (0)	1 (1)	1 (1)	0 (0)	4 (7)	0 (0)
Halfmoon Pond	7/24 – 7/27/99	12	0 (0)	1 (2)	0 (0)	0 (0)	1 (1)	1 (1)
HHH	8/6 – 8/9/99	1	0 (0)	0 (0)	0 (0)	0 (0)	1 (4)	0 (0)
Hunter's Brook South	8/6 – 8/9/99	22	0 (0)	7 (10)	0 (0)	1 (1)	17 (185)	0 (0)
Leech	7/12 – 7/15/99	24	1 (1)	2 (3)	0 (0)	0 (0)	16 (33)	9 (19)

Table C.3 continued.

Site	Date Sampled (month/day/year)	Number of Stations	*Ambystoma maculatum*	*Notophthalmus viridescens*	*Pseudacris crucifer*	*Rana palustris*	*Rana clamitans*	*Rana catesbeiana*
Lifesaver	7/30 – 8/2/99	6	0 (0)	1 (3)	0 (0)	0 (0)	6 (52)	0 (0)
Mac's	7/18 – 7/21/99	17	3 (4)	4 (11)	0 (0)	3 (11)	8 (16)	1 (1)
North of Pinnochio	7/30 – 8/2/99	14	0 (0)	2 (3)	0 (0)	3 (5)	6 (6)	0 (0)
North of Witch Hole Pond	7/24 – 7/27/99	11	5 (12)	3 (3)	0 (0)	1 (3)	4 (4)	0 (0)
Pinnochio	7/30 – 8/2/99	11	0 (0)	2 (2)	0 (0)	0 (0)	1 (1)	2 (2)
Richardson Brook Beaver	7/18 – 7/21/99	12	1 (2)	2 (2)	0 (0)	0 (0)	9 (13)	0 (0)
Richardson Brook UB	7/18 – 7/21/99	5	2 (2)	1 (2)	0 (0)	0 (0)	4 (7)	0 (0)
Schooner Head Road Beaver	7/30 – 8/2/99	2	0 (0)	1 (1)	0 (0)	0 (0)	1 (7)	0 (0)
South of The Tarn	7/30 – 8/2/99	15	0 (0)	5 (17)	0 (0)	2 (11)	6 (79)	0 (0)
Stick Wetland	7/24 – 7/27/99	16	1 (1)	2 (2)	0 (0)	1 (1)	5 (7)	0 (0)
Swallowtail	7/18 – 7/21/99	12	0 (0)	7 (20)	0 (0)	1 (1)	9 (24)	0 (0)
Top of the Hill Tarn	7/30 – 8/2/99	7	3 (3)	1 (1)	1 (1)	1 (2)	7 (30)	0 (0)

Table C.4. Number of stations that each species of larval amphibian was captured at during bottle trap sampling in 30 ponds in Acadia National Park, 1999. Total number of individuals captured is indicated in parentheses.

Site	Date Sampled (month/day/year)	Number of Stations	*Ambystoma maculatum*	*Notophthalmus viridescens*	*Pseudacris crucifer*	*Rana palustris*	*Rana clamitans*	*Rana catesbeiana*
B75	7/24 – 7/27/99	2	0 (0)	1 (2)	0 (0)	0 (0)	0 (0)	0 (0)
B99	7/24 – 7/27/99	2	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)
Breakneck Pond	7/18 – 7/21/99	24	1 (1)	0 (0)	0 (0)	1 (1)	0 (0)	2 (2)
Bruce's vp	7/12 – 7/15/99	5	3 (4)	0 (0)	1 (1)	0 (0)	1 (1)	0 (0)
C41	7/24 – 7/27/99	4	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
107	7/24 – 7/27/99	1	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
113	7/24 – 7/27/99	2	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
183	8/6 – 8/9/99	1	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)
Duck Pond	8/6 – 8/9/99	8	0 (0)	0 (0)	0 (0)	0 (0)	4 (10)	0 (0)
East of Fawn Pond	7/13 – 7/16/99	20	3 (4)	0 (0)	0 (0)	0 (0)	3 (6)	0 (0)
18	7/18 – 7/21/99	1	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)
Fawn Pond	8/6 – 8/9/99	18	0 (0)	1 (1)	0 (0)	0 (0)	2 (3)	5 (5)
Gilley Beaver	8/6 – 8/9/99	1	0 (0)	1 (1)	0 (0)	0 (0)	1 (8)	0 (0)
Gorge Trail Beaver	7/12 – 7/15/99	5	1 (1)	0 (0)	0 (0)	0 (0)	2 (4)	0 (0)
Halfmoon Pond	7/24 – 7/27/99	12	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)
HHH	8/6 – 8/9/99	1	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Hunter's Brook South	8/6 – 8/9/99	22	1 (1)	4 (8)	0 (0)	0 (0)	17 (75)	0 (0)
Leech	7/12 – 7/15/99	24	0 (0)	0 (0)	0 (0)	0 (0)	7 (36)	2 (2)

Table C.4 continued.

Site	Date Sampled (month/day/year)	Number of Stations	*Ambystoma maculatum*	*Notophthalmus viridescens*	*Pseudacris crucifer*	*Rana palustris*	*Rana clamitans*	*Rana catesbeiana*
Lifesaver	7/30 – 8/2/99	6	0 (0)	1 (2)	0 (0)	0 (0)	3 (4)	0 (0)
Mac's	7/18 – 7/21/99	17	0 (0)	1 (1)	0 (0)	0 (0)	1 (1)	0 (0)
North of Pinnochio	7/30 – 8/2/99	14	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
North of Witch Hole Pond	7/24 – 7/27/99	11	2 (2)	0 (0)	0 (0)	0 (0)	3 (4)	0 (0)
Pinnochio	7/30 – 8/2/99	11	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)	1 (1)
Richardson Brook Beaver	7/18 – 7/21/99	12	1 (1)	1 (1)	1 (2)	0 (0)	3 (11)	0 (0)
Richardson Brook UB	7/18 – 7/21/99	5	2 (3)	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)
Schooner Head Road Beaver	7/30 – 8/2/99	2	0 (0)	1 (5)	0 (0)	0 (0)	1 (1)	0 (0)
South of The Tarn	7/30 – 8/2/99	15	0 (0)	3 (4)	0 (0)	1 (1)	2 (20)	0 (0)
Stick Wetland	7/24 – 7/27/99	16	0 (0)	3 (3)	0 (0)	0 (0)	0 (0)	0 (0)
Swallowtail	9	12	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)
Top of the Hill Tarn	7/30 – 8/2/9	7	0 (0)	0 (0)	0 (0)	0 (0)	6 (14)	0 (0)

BIOGRAPHY OF THE AUTHOR

Mary Beth Kolozsvary was born in Syracuse, New York on September 30, 1965. She was raised in Syracuse and graduated from Henninger High School in 1983. She attended the SUNY – College of Environmental Science and Forestry and graduated in 1988 with a Bachelor's degree in Forest Biology. She worked for a variety of agencies for the next several years, including the New York State Department of Environmental Conservation, United States Forest Service, The Institute for Wildlife and Environmental Toxicology, and The Peregrine Fund. She attended Purdue University, Department of Forestry and Natural Resources, and graduated in 1998 with a Master's degree. Her Master's research involved investigating the effects of agriculturally induced fragmentation on amphibian assemblages in west-central Indiana. She has published articles in Canadian Journal of Zoology, Ecological Applications, and Diversity and Distributions.

Mary Beth recently began a position as a Biodiversity Specialist at the New York State Biodiversity Research Institute in Albany, New York. She is currently a member of the Ecological Society of America, Society for Conservation Biology, Society for the Study of Amphibians and Reptiles, and Society of Wetland Scientists. She is a candidate for the Doctor of Philosophy degree in Ecology and Environmental Sciences from The University of Maine in August, 2003.