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# Wetland and Nest Scale Habitat Use by the Four-toed Salamander (*Hemidactylium scutatum*) in Maine, and a Comparison of Survey Methods

Rebecca J. Chalmers

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**WETLAND AND NEST SCALE HABITAT USE BY THE FOUR-TOED  
SALAMANDER (*Hemidactylium scutatum*) IN MAINE,  
AND A COMPARISON OF SURVEY METHODS**

By

Rebecca J. Chalmers

B.A. Marlboro College, 1998

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Ecology and Environmental Science)

The Graduate School

The University of Maine

December, 2004

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**WETLAND AND NEST SCALE HABITAT USE BY THE FOUR-TOED  
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Thesis Advisor: Dr. Cynthia S. Loftin

An Abstract of the Thesis Presented  
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December, 2004

Conserving amphibian populations requires knowledge of a species and its habitat relationships. The four-toed salamander (*Hemidactylium scutatum*) is listed as *Special Concern* in Maine and 11 additional states and provinces, *Threatened* in Illinois, and *Endangered* in Indiana (Appendix A). Little is known of *H. scutatum* ecology despite the species' extensive range. Infrequent sightings of *H. scutatum* throughout its range may indicate either low numbers or that the species' behavior make detection difficult. Records for *H. scutatum* in Maine existed from only 32 sites before my study, and the total number of occurrences of this species in Maine is unknown (P. deMaynadier, Maine Department of Inland Fisheries and Wildlife, personal communication). I found 238 four-toed salamander nests in 36 wetlands, which were new sites. The survey protocol, natural history descriptions, and definitions of wetland and shoreline habitat presented will increase detections of this species and thus improve the monitoring and management of *H. scutatum* and the wetland habitat that this species occupies.

In the first chapter, I compare monitoring techniques for the species, document new points in which I found the species, and present natural history information. I conducted surveys of adults on roads during rainy spring nights, surveys of nests, and surveys of larvae with dipnetting in wetlands, and I present incidental visual encounters and pitfall captures for comparison. Greatest numbers of salamanders were found with the nest surveys, which were conducted in palustrine wetlands by walking in the water and parting the shoreline vegetation to search for eggs and attendant females. I found *H. scutatum* nests in 35 of 92 wetlands intensively searched.

In the second chapter, I investigate species-habitat relationships that predict *H. scutatum* presence at two scales: the wetland (and surrounding landscape) and the available shoreline points in which nests could occur. I collected data at wetlands with and without nests, and I collected data along the shoreline at points with and without nests. With these data, I created models that predicted wetlands with nests, and I created and evaluated models that predicted nest point selection within a wetland and available point characteristics between wetlands with and without nests. Wetlands with nests were best predicted by higher pH and were negatively associated with shrub scrub and unconsolidated bottom NWI classes. Wetlands with nests were also predicted by the availability of shoreline points that provided *Sphagnum* spp. for egg attachment, wood substrate, water flow, the presence of blue-joint reed grass (*Calamagrostis canadensis*), meadowsweet (*Spiraea alba*), steplebush (*Spiraea tomentosa*), and sensitive fern (*Onoclea sensibilis*), and the absence of sheep laurel (*Kalmia angustifolia*) and deciduous forest NWI class. Within wetlands with nests, shoreline points with nests were best distinguished from shoreline points without nests by steeper shores, greater near-shore

and basin water depth, deeper nesting vegetation, presence of moss and winterberry (*Ilex verticillata*), and a negative association with *Spiraea alba*, leatherleaf (*Chamaedaphne calyculata*), and *Kalmia angustifolia* within 1 m of the shoreline point.

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**ECOLOGY AND SURVEY METHODS FOR THE FOUR-TOED  
SALAMANDER (*Hemidactylium scutatum*)**

**CHAPTER ABSTRACT**

I used 3 survey methods (surveys of adults on roads during rainy spring nights, surveys of nests along wetland shoreline vegetation, and dipnetting for larvae) to document location and natural history of four-toed salamanders (*Hemidactylium scutatum*) in Maine during March to August, 2001-2004. Incidental visual encounters and pitfall captures of the species are presented for comparison. Greatest numbers of salamanders were found during nest surveys, which were complete searches of shoreline vegetation in palustrine wetlands. I found 238 *H. scutatum* nests in 36 of the 92 wetlands searched. The survey protocol and natural history descriptions should aid in detecting this species and thereby improve monitoring and management of *H. scutatum*.

**INTRODUCTION**

Determining appropriate methods to survey amphibian populations has become increasingly important because of worldwide declines in amphibian populations (Heyer et al. 1994, Houlahan et al. 2000). Amphibian population declines are occurring even on apparently protected lands for uncertain or complex reasons [e.g., populations of 25 anuran species in Costa Rica's Monte Verde Cloud Forest Preserve declined in 1987 and were not detected in 1990 (Pounds et al. 1997) and, in Australia, populations of 24 species declined 90% in 3 months (Laurance et al. 1996)].

Amphibians are ecologically important as predators and prey in a diversity of ecosystems. Biomass of amphibians can be substantial [e.g., salamander biomass is equal to that of small mammals and double that of birds in New Hampshire forests (Burton and Likens 1975) and densities of *Eleutherodactylus coqui* frogs in Puerto Rico average 20,570 per hectare (Stewart 1991)]. As ectotherms, amphibians transfer a disproportionately large amount of energy to the next trophic level (Pough 1980).

Amphibians may be especially sensitive to environmental integrity (e.g., toxins) because of their complex life cycle, close association with water, relative longevity, and microhabitat specificity. Their complex life cycle includes several life stages with different physiological and ecological requirements and several metamorphoses during which individuals may have heightened sensitivity to toxins. Amphibians have permeable skin throughout their life cycle and frequently live in water during at least one life stage. The microhabitat specificity and low mobility of amphibians means their health is closely linked to the immediate environment. Polluted atmospheric deposition is absorbed through the skin of amphibians before the contaminants have been buffered by soil or water. The relative longevity and carnivorous feeding habits of many amphibians can make them susceptible to accumulated toxins. Amphibian population declines may thus indicate pervasive environmental toxins and other human caused problems that will also affect other organisms.

It has been difficult to confirm population declines because of a lack of long-term population monitoring data, a lack of count data over large spatial scales, and limited ecological knowledge of many species. Assessing the health of amphibian populations requires proven survey protocols and knowledge of species-habitat relationships. Survey

protocols are based on the ecology of a species, including knowledge about how and where to find animals.

Sufficient knowledge of a species' seasonal habits and life stages are needed to reliably and repeatedly assess amphibian population trends. Species that are widely dispersed in low densities or are clustered disjunctly across the landscape may require specialized search methods to detect their presence. Currently no protocol exists for surveying *H. scutatum*. Little is known of this species' ecology, and this lack of information is a major impediment to formulating recommendations to manage or sample this species. Infrequent sightings of *H. scutatum* across its range may indicate either low numbers or behavior that makes animals difficult to find. I examined commonly used methods for surveying amphibian species presence (e.g., surveys of adults on roads during rainy spring nights, surveys of nests in vegetation along wetland shoreline, dipnetting for larvae) to determine the most efficient means to locate *H. scutatum*, and I sought to increase knowledge about this species' ecology.

\* *H. scutatum* (Family Plethodontidae) adults are lungless invertivores that are found under debris in forests throughout the year and brooding females are found in wetlands during the nesting season (Petranka 1998). The species' occurrence is patchy (Petranka 1998). Breeding occurs in late summer through fall (Bishop 1941), and females migrate to breeding wetlands in spring (or winter in the southern portion of their range) to lay their eggs in vegetation, typically *Sphagnum* spp., on wetland shores (Harris in press). Nests may contain eggs from more than one female, but usually only one female will brood the eggs until hatching (Petranka 1998). Females may not breed every year (Harris and Ludwig 2004). Larvae are aquatic, carnivorous, and cryptic (Petranka

1998). It is not known when juveniles migrate to uplands or where they over-winter, and little is known of either juvenile or adult ecology.

Conducting surveys of amphibians on roads during rainy nights in the spring is a technique used to target concentrations of amphibians migrating to breeding pools. This survey method provides information on breeding phenology and approximate sites of terrestrial and wetland habitats used by amphibians. Roads serve as line transects and provide an open substrate on which amphibians are readily seen (Shaffer and Juterbock 1994). Roads with low traffic volume that are adjacent to wetlands are particularly suitable. Typically, only gravid *H. scutatum* are detected during surveys on roads during rainy spring nights. As the season progresses, females and juveniles may be observed returning to upland areas and, occasionally, individuals can be found on roads on warm nights at other times of year.

Female *H. scutatum* do not leave the nest site while attending their eggs and may remain with their eggs for the full period of 38 - 62 days of embryo development (Petranka 1998). During this time, attending females are potentially concentrated in specific habitats and could provide information on population numbers and breeding behavior. I systematically searched wetland shorelines for nesting salamanders. Because I searched all available shoreline of a wetland, it was likely that I detected most nests.

*H. scutatum* larvae are adapted to lentic, low oxygen environments (Petranka 1998). The larvae are classified as “pond-type larvae”, defined by large, bushy external gills and a long fin fold that extends well up onto the body near the shoulder region (Petranka 1998). Other species in the study area that are pond-type larvae include *Ambystoma* spp. and red spotted newts (*Notophthalmus viridescens*). *Ambystoma* spp.

develop earlier than *H. scutatum* larvae, but larval *N. viridescens* can co-occur at the same size classes as *H. scutatum* larvae, making field identification difficult. Species identification of larval *H. scutatum* is complicated by the variable numbers of toes (0-4) at different stages of development (*personal observation*, Bishop 1941). I observed larvae to improve survey techniques, although I did not conduct systematic searches for larvae. I contrasted traits of *H. scutatum* larvae with those of *N. viridescens* and recorded dates observed in order to describe the duration of the larval period.

## **METHODS**

### **Study Area**

I conducted surveys of adults, nest, and larvae in Acadia National Park (ANP), Maine. I conducted surveys of adults and nests at the University of Maine Demeritt Forest (DF), and surveys of nests at University of Maine Foundation Penobscot Experimental Forest (PEF), USFWS Sunkhaze Meadows National Wildlife Refuge (SMNWR), and USDA Forest Service Northeastern Research Station Massabesic Experimental Forest (MEF). All units are conservation lands with first and second growth mixed forest. Common wetland communities (based on the National Wetland Inventory classification system; Cowardin et al. 1979) include shrub peatland, deciduous forest, coniferous forest, aquatic bed, and freshwater marsh (Calhoun et al. 1994). Wetland ecological communities of Maine are described in detail by NatureServe (2004). Maine climate is cool and humid, with a mean annual (1895-2003) temperature of 5.1°C, the lowest average monthly temperature of -9.7°C in January, and the highest average

monthly temperature of 19.1°C in July (NOAA 2004). The mean annual (1895-2003) precipitation is 114 cm (NOAA 2004).

Acadia National Park (19,182 ha) borders the Atlantic Ocean and is managed for the conservation of scenery, natural and historic objects, and wildlife. Disturbances in ANP include a widespread fire in 1947 and aerial applications of DDT and Malathion during the 1950s and 1960s (J. Hazen-Connery, National Park Service, personal communication). Atmospheric deposition of a variety of pollutants affects all study areas (e.g., Weathers et al. 2003, Tanabe 2003, Heath et al. 1993). Long-term forestry research and education are the management goals at DF (809 ha), PEF (1540 ha), and MEF (1456 ha). Disturbance regimes of MEF include farmland conversion in the 1900s, white pine (*Pinus strobes*) plantings in the 1930s, an extensive burn in 1947, and herbicide (2,4,5-T and 2,4-D) application during the 1940s to 1960s (MEF website 2004). Sunkhaze Meadows National Wildlife Refuge is managed for fish and wildlife and encompasses a wetland complex around a major stream, several feeder streams, and the second largest peatland in Maine.

In my study areas, historical records for this species included 1 observation of *H. scutatum* in MEF (A. Dibble, University of Maine, personal communication) and 1 historical (1960) and 15 recent observations of individuals crossing roads during the spring in ANP (B. Connery and J. Gormley, National Park Service, personal communication). No nest locations or larvae were previously recorded.

### **Surveys of Adults on Roads During Rainy Spring Nights**

I searched between dusk (approximately 1930 h) and 0100 h during rainy or misty nights ( $n = 16$ ) of March, April and May 2001-2004. I walked along roads with a NiMH

bicycle light and a spare battery that provided up to 4 hours of intense light to search for salamanders. I did not measure individuals because of time constraints, and sexing by “candling” individuals did not illuminate eggs. I discovered salamanders leaving tail-drag tracks in roadside grit during one night. *H. scutatum* left narrow, straight (e.g., perpendicular to the road) tail-drag tracks that were continuous. Red-backed salamander (*Plethodon cinereus*) tracks were the same width but were not straight, and spotted salamander (*Ambystoma maculatum*) tracks were straight, but were wider. Search effort was quantified as number of minutes spent searching per person (if one or two observers); greater numbers of observers (i.e., volunteers) were counted as only two people for effort quantification purposes, because they covered the same amount of area as two individuals.

Surveys of adults on roads during rainy spring nights were conducted in and around ANP during 2001 and 2002 and on a paved bike path in DF during 2002-2004. Other study units were not surveyed with this method, because they either lacked roads or were too far away to coordinate surveys with appropriate weather conditions. Roads surveyed in ANP had low traffic volume, were located throughout the island, were flat, and bordered coniferous and deciduous forests containing a variety of wetland types (Calhoun et al. 1994). A known migration location, Duck Brook Road, was surveyed on 12, 19, and 21 April; 15 May, 2001; and 3 March, 1, 3, 8, and 17 April, 2002. Duck Brook road parallels a stream and wetland complex located downhill from the road and a deciduous forest on the upland side. Other roads surveyed (during 13, 19, and 21 April, and 15, 22, and 28 May, 2001) include Blackwoods Campground, Breakneck Road, Oak Point Road, Long Pond Fire Road, Cromwell Drive, Norway Drive, Loop Road, Whitney

Farm Road, Crooked Road, Pretty Marsh Road, and the Jessup and Great Meadows trails. I report results of another searcher who conducted surveys during 2001-2003 at Sand Point Road, a known migration location near ANP (J. Gormley, Acadia National Park, unpublished data). A paved bike path in DF was surveyed 23 April, 2003 (J. Crocker and S. Barteaux); 3 April, 2002; and 13, 14 April, and 2 and 3 May, 2004 (R. Chalmers).

### **Surveys of Nests**

I initiated surveys for brooding salamanders the week migration started, providing time for gravid females to locate a nest point and to deposit eggs. Wetlands surveyed during the first week following migration were re-surveyed later. I surveyed other wetlands only once during the nesting season.

I quantified search effort as the minutes each observer actively searched for salamander nests, excluding time needed to record data. I assumed the entire shore of most wetlands was available to a female migrating to the wetland, because *H. scutatum* can swim well (*personal observation*, Harris in press). I searched all vegetation along the shore within 30 cm of the water, including hummocks, islands, and bases of trees and shrubs. Initial searches in 2001 extended 1 m onto shore. I reduced this distance when no nests were found > 30 cm from water. The search area widened during the brooding period as water levels receded more than 30 cm from the basin edge. Search procedures included gently but deeply parting vegetation without tearing, to expose eggs and attendant females. Although nests with females were easiest to detect, I also detected unattended nests with as few as one egg. Upon completion of a wetland survey, I disinfected equipment with a spray of 10% bleach solution and rinsed with water to minimize potential transmission of disease agents among wetlands.

I conducted preliminary surveys for nests in 40 wetlands in ANP during 28 May-18 June, 2001, to develop the search method. I conducted complete, timed surveys for nesting *H. scutatum* in 67 wetlands on study units (ANP, MEF, PEF, DF, and SMNWR) during 2002 and 2003. I surveyed 30 wetlands in ANP during 27 April - 21 June, 2002 and I surveyed wetlands in ANP ( $n = 12$ ), MEF ( $n = 16$ ), PEF ( $n = 4$ ), DF ( $n = 3$ ), and SMNWR ( $n = 2$ ) during 23 April - 24 June, 2003. I created a map of all NWI-mapped palustrine wetlands in the study area and numbered each wetland or, in the case of wetlands too large ( $> 11$  ha) to search in a day, I numbered sections of wetlands with the same NWI class. I used a random number table to select numbered wetlands from each study area. I searched 56 wetlands that were randomly selected, and I searched 11 additional wetlands when opportunistic surveys revealed presence of *H. scutatum*, balancing my sample size of wetlands with and without nests (Chapter 2). Area searched per wetland ranged from 0.03 ha to 10.92 ha, with a mean of 1.17 ha ( $SD = 1.54$  ha;  $n = 67$ ).

### **Description of Larvae**

I collected 2 eggs and maintained them to hatching in 2001 to study and determine characteristics that could be used to identify larvae in the field. *H. scutatum* larvae had not previously been recorded in Maine and because the species is listed as a species of *Special Concern*, I was granted permission by ANP to collect only 2 larvae. Organic matter and water from the natal pond provided food for the developing larvae. Larval *N. viridescens* were also raised in aquaria, or captured from 1 wetland in ANP, for comparison. Additionally, I searched for larvae in ANP (3 wetlands 26 July, 2001; 2 wetlands 29 July, 2002; and 2 wetlands 30 July, 2003) to quantify search effort, describe

larvae, and estimate date of metamorphosis. I searched for larvae in 1 wetland in DF (27 June and 22 July, 2004) to photograph larvae. Most wetlands not surveyed were dry. Wetlands in which larvae were found were those with highest numbers of nests (6 - 33) and small pools of remaining water at the time of metamorphosis, which facilitated capture of larvae. Water, muck, and larvae were collected from the pools with a bucket, sieved through a dipnet, and larvae were transferred to water-filled plastic bags for measurement.

### **Phenology**

Phenology of migration, nest initiation, hatching, and metamorphosis varies with local habitat and weather patterns. Phenological observations from different study areas were combined to determine the time interval over which subsequent observations are likely to be made. In spring, when *H. scutatum* migration to nesting pools occurs, weather fronts typically bring precipitation that initiates migration, generally at the same time in southern, coastal, and inland regions of Maine unless local habitats are still frozen.

### **RESULTS**

I found 10 *H. scutatum* and 10 tracks during surveys of adults on roads during rainy spring nights, 212 nests and 172 attendants during surveys of nests, and 13 larvae when dipnetting (Table 1.1). The largest number of *H. scutatum* observed, the largest number per search hours of effort, and the largest number of previously unknown populations, were detected with surveys of nests (Table 1.1).

Table 1.1. Surveys of *H. scutatum* adults on roads during rainy spring nights, nests (eggs and sometimes attendant females) in vegetation along wetland shoreline, and aquatic larvae captured with dipnetting in Maine, 2001-2004

Survey method	Number of sites searched	Number of sites observed	Number of salamanders	Person-hours searched	Range of dates observed
Adults and tracks on roads <sup>a</sup>	14	2	10 Adults 10 Tracks	49	4/8 - 5/28
Nests along shoreline <sup>b</sup>	67	35	212 Nests 172 Attendants 4266 Eggs	137	4/27 - 6/16 4/27 - 5/6 Ovposit 6/16 - 7/9 Hatch
Larvae in wetlands <sup>c</sup>	2	2	13 Larvae	40	6/16 - 7/30 7/27 - 7/30 Metamorph

<sup>a</sup> ANP (2001, 2002), DF (2003)

<sup>b</sup> ANP (2002, 2003), DF, PEF, SMNWR, and MEF (2003)

<sup>c</sup> ANP (2002, 2003)

## Surveys of Adults on Roads During Rainy Spring Nights

*H. scutatum* migrated during the first rainy nights of spring with air temperatures of 9.4°, 10°, 12.5°, and 16°C. Migration was not observed during colder (e.g., 2° - 9°C) nights of precipitation, which occurred while the earth was still frozen. I found 10 *H. scutatum* and 10 tracks during 5 of 16 nights that I searched with 49 person-hours of effort during 2001 - 2004 (Table 1.1).

Although their search effort was not quantified (Table 1.2), other observers detected an additional 13 *H. scutatum*. *H. scutatum* were detected crossing roads 8 April through 3 May during the pre-nesting season and from 28 May through 24 June, after nesting had begun.

Other species encountered on roads during *H. scutatum* movements included *P. cinereus* ( $n = 62$ ), *A. maculatum* ( $n = 35$ ), spring peeper (*Pseudacris crucifer*) ( $n = 23$ ), *N. viridescens* ( $n = 1$ ), blue spotted salamander (*Ambystoma laterale*) ( $n = 1$ ), wood frog (*Rana sylvatica*) ( $n = 3$ ), and leopard frog (*Rana pipiens*) ( $n = 1$ ). Species observed mating during *H. scutatum* migration included wood frogs, spring peepers, and spotted salamanders.

## Surveys for Nests

I found nests as early as 27 April and as late as 9 July. I found 238 *H. scutatum* nests, 193 attendant females, and 4,968 eggs in wetlands searched during 2001-2003. I found 32 adults and 6 juveniles (i.e., < 22 mm snout to vent length) not associated with nests. *H. scutatum* were present at 36 (39%) of 92 wetlands surveyed (Table 1.3). 67 wetlands (35 with and 32 without nesting *H. scutatum*) were intensively surveyed to research *H. scutatum* nesting habitat use (Chapter 2).

Table 1.2. Numbers of *H. scutatum* adults counted on roads and a bike path during rainy spring nights in Maine, 2001-2004.

Location	Date	# Salamanders <sup>a</sup>	# Tracks	Observer
Duck Brook Rd.	4/21/01	4	10	Chalmers
“	4/8/02	3	0	Chalmers
Sand Point Rd.	4/24/01	1	0	Gormley
“	5/15/01	1	0	Gormley
“	6/24/01	1	0	Gormley
“	4/13/02	1	0	Gormley
Oak Point Rd.	5/28/01	1	0	Chalmers
DF bike path	4/23/03	9	0	Crocker, Barteaux
“	5/2/04	1	0	Chalmers
“	5/3/04	1	0	Chalmers

<sup>a</sup> The number of salamanders is greater than in Table 1.2 because of inclusion of data collected by other searchers who did not quantify their search effort.

Table 1.3. Numbers of *H. scutatum* nests at study wetlands in Maine, 2001-2003.

Land unit	Year	# Wetlands searched	# Wetlands in which nests detected	# Nests	#Attendant females
ANP	2001	40 <sup>a</sup>	7	26	21
ANP	2002	30 <sup>a</sup>	11	109	84
ANP	2003	12 <sup>a</sup>	8	36	30
MEF	2003	16	8	40	35
SMNWR	2003	2	1	2	0
PEF	2003	4	4	11	9
DF	2003	3	3	14	14
Total		92 <sup>b</sup>	36 <sup>c</sup>	238	193

<sup>a</sup> Of the 40 wetlands searched during 2001 in ANP, 11 were re-surveyed in 2002 and 4 were re-surveyed in 2003.

<sup>b</sup> A total of 92 wetlands were searched during 2001-2003, but because some wetlands were surveyed twice, a total of 107 searches were conducted .

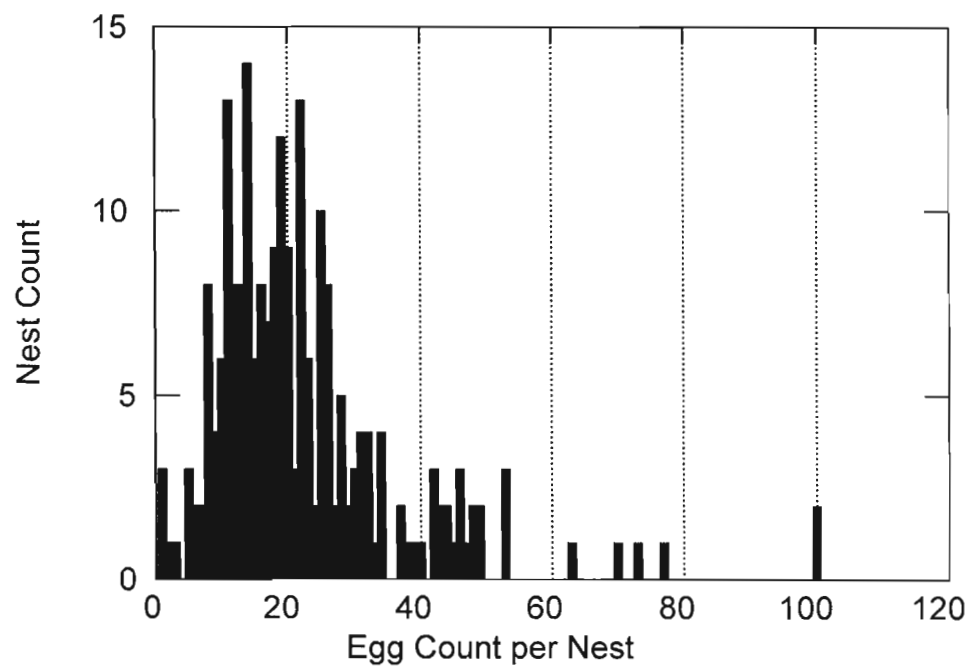
<sup>c</sup> A total of 36 wetlands containing nests were detected, but because some wetlands were surveyed twice, a total of 42 surveys in wetlands with nests were conducted.

**Attendants.** *H. scutatum* females were present at 81.1% of the 238 nests located. One nest was attended by 2 females, and twice females were found between a pair of nests < 2 cm apart. Females attended eggs for varying periods, but none were observed with hatching embryos. Attendant females usually remained at nests after being disturbed by the searcher. Attendant females remained at the nest and were easily handled when temperatures were < 10°C. As air temperatures increased, females crawled away or dropped into the water within seconds, but returned to nests within approximately 5 minutes. Snout vent length (SVL) of attendant *H. scutatum* ( $n = 158$ ) was (mean  $\pm$  SD mm)  $33.3 \pm 2.5$ , and total length (TL) averaged  $67.6 \pm 7.1$ . Body length accounted for a mean of 78% of TL. The smallest attendant females with undamaged tails were 27.5/56.5 mm (SVL/TL) and 31.0/52.0 mm (SVL/TL), and the largest were 41.0/80.0 mm (SVL/TL) and 37.0/87.0 mm (SVL/TL).

**Nest point re-use.** One nest point was occupied by a nesting *H. scutatum* in the same 1 cm<sup>2</sup> location for 3 consecutive years, although it is unknown if the same female occupied the nest. At other points, nests were in the same location for 2 consecutive years.

**Egg count.** Number of eggs per nest ranged from 1 to 100; the mean equaled 22.5 ( $SD = 14.9$ ,  $n = 221$ ), and the median was 19 eggs (Figure 1.1). The fewest eggs in a complete, attended clutch were 5. A stem-and-leaf plot of egg count per nest showed nests with > 45 eggs as outlying values. These nests may have been communal, as the maximum clutch size is estimated to be 65 eggs in Virginia (Harris et al. 1995), whereas, in New York nests with > 40 eggs were considered joint clutches (Gilbert 1941). Based on Harris et al. (1995), nests that may have contained multiple clutches in the study included 5 nests (2.3 %) with greater than 65 eggs (i.e., 70, 73, and 77 eggs and two clutches with

Figure 1.1. Clutch size of *H. scutatum* nests in Maine, 2001-2003.



100 eggs). Based on a 40-egg threshold, 25 nests (11.3 %) may have been joint clutches.

***Development at hatching.*** Embryos hatched soon after reaching Harrison stages 41 - 46 (Harrison 1969) when they had a black pupil, a bronze or gold flecked iris, and an eyeline on each side of the eye. A Y-shaped dark mark developed on the forehead between the eyes. The jelly changed its consistency from firm to oozing, and the large gills became brown or orange-red. The ventral surface was cream or white and clearly distinguished from the dorsum, which was tan with a dark lattice pattern and pale spots. The red heart and other internal organs became visible. Front and rear legs ranged from limb buds to well-developed appendages and the body and tail lengthened. Salamander embryos could turn in the egg, sometimes into an “S” shape.

***Hatching.*** I did not quantify hatching success, but observations of egg development suggested that most eggs hatched. The timing of hatching often coincided with drying of wetlands, suggesting that survival of larvae would be affected (e.g., 8 of 9 wetlands with *H. scutatum* nests in DF and PEF had no water remaining in them within two weeks of hatching in 2003). Other potential causes of egg death included flooding of nests, which was observed in one wetland, that may lead to rot or premature hatching (Petranka 1998, but see Wood 1953). Although *H. scutatum* eggs are unpalatable to carabid beetles (Hess and Harris 2000), a larval *Megaloptera* sp. that was observed in a recently occupied nest cavity may have preyed on one nest. I observed embryos hatching from nests during 16 June - 9 July in 2002 and 2003.

***Placement of nests.*** Nests ( $n = 217$ ) were positioned (mean  $\pm$  *SD* cm)  $10.4 \pm 5.8$  above water. Water depth below nests was  $15.3 \pm 17.2$  ( $n = 210$ ), and the maximum depth within 2 m of nests was  $33.6 \pm 28.5$  ( $n = 208$ ). Nest vegetation depth was  $11.4 \pm 5.2$  ( $n =$

194). Slope angle from water surface up the shoreline to the nest location was  $76.6^{\circ} \pm 14.8$  ( $n = 195$ ). Additional information on nest placement, egg attachment, and surrounding vegetation is presented in Chapter 2.

**Nest vegetation.** Vegetation surrounding eggs was usually moss (217 of 220 nests; 98.6%) and typically *Sphagnum* spp. ( $n = 182$ ). Eggs were usually attached to the portion of moss in which recent green growth merged with older tan growth ( $n = 87$  nests). Eggs were also attached to only recent green growth ( $n = 16$ ), only older tan growth ( $n = 50$ ), and only dark brown decomposing moss or roots (e.g., tree roots, sedge roots, shrub rootlets, and woody debris) ( $n = 36$ ). Non-moss nest vegetation ( $n = 23$ ) included blue-joint reed grass (*Calamagrostis canadensis*) ( $n = 5$ ), tussock sedge (*Carex stricta*) ( $n = 2$ ), poison ivy (*Rhus radicans*) ( $n = 1$ ), royal fern (*Osmunda regalis*) rhizomes ( $n = 1$ ), wood ( $n = 9$ ), liverwort (Class Hepaticae) ( $n = 2$ ), cinnamon fern (*Osmunda cinnamomea*) stalk litter ( $n = 1$ ), deciduous leaf litter ( $n = 1$ ), and leatherleaf (*Chamaedaphne calyculata*) rootlets ( $n = 1$ ).

**Substrate.** Substrate supporting nest vegetation was provided by woody debris ( $n = 99$ ), living vegetation ( $n = 89$ ), soil ( $n = 16$ ), and rock ( $n = 5$ ). Wood included stumps, logs, upturned roots, and branches. Living vegetation included many species of trees [e.g., red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*), eastern white cedar (*Thuja occidentalis*), spruce (*Picea* spp.), balsam fir (*Abies balsamea*)] and shrubs [e.g., winterberry (*Ilex verticillata*), leatherleaf (*Chamaedaphne calyculata*), male berry (*Lyonia ligustrina*), highbush blueberry (*Vaccinium corymbosum*), mountain holly (*Nemopanthes mucronata*), sweet gale (*Myrica gale*), alder (*Alnus* spp.), meadowsweet (*Spiraea alba*), and steeplebush (*Spiraea tomentosa*)], which provided support with their

trunks or stems for moss to grow. Cinnamon fern (*Osmunda cinnamomea*) and royal fern (*Osmunda regalis*) rhizome mounds created shoreline relief and, additionally, the litter from the ferns created moist structural habitat in which to lay eggs. Additional plants that supported nests included tussock sedge (*Carex stricta*), blue joint reed grass (*Calamagrostis canadensis*), narrow-leaf cattail (*Typha angustifolia*) stalks, and moss (*Sphagnum* spp.).

**Nest density.** I found a median of 5 nests per wetland (Table 1.4) and an average of 5.7 nests (range = 0-33;  $SD = 5.7$ ;  $n = 35$ ) per wetland. The density of nests in wetlands ( $n = 35$ ) was a mean of 0.00137 nests per square meter, or 4,774 m<sup>2</sup> per nest, of total searched area, including open water. Wetlands ranged in size from 817 to 42,361 m<sup>2</sup> ( $\bar{x} = 12,338$ ;  $SD = 10,421$ ;  $n = 35$ ).

Table 1.4. Number of *H. scutatum* nests per wetland ( $n = 35$ ) in Maine, 2001-2003, shown by a stem-and-leaf plot.

```

1. 00000 (Minimum)
2. 00000 (Lower hinge)
3. 0000
4. 00
5. 000000 (Median)
6. 000
7. 00000 (Upper hinge)
8.
9.
10. 0
11. 0
12.
13. 00
* * * Outside Values * * *
33. 0 (Maximum)
```

## Netting and Identification of Larvae

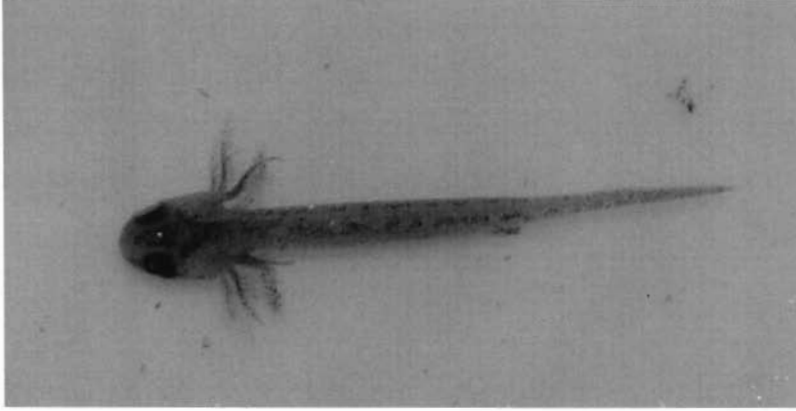
**Dipnetting.** I netted 13 wild larvae with 40 hours of search effort (Table 1.1) in wetlands in which the species was known to be present.

**Captive larvae.** I collected 2 *H. scutatum* eggs in 2001 from an ANP wetland and incubated them in sphagnum moss suspended above water in an aquarium. I observed embryos hatching (wriggling sideways down to water) from nests on 18 June. At hatching, larvae were 10 mm in TL, less than the 11 - 14 mm length reported by Bishop (1941). By 9 July the larvae were translucent yellow-brown, 10 mm SVL and 18 - 19 mm TL, and one larva had visible rear toes. Within 8 days (17 July), larvae were 19 mm TL with a dorsal fin extending onto the body. Larvae metamorphosed (red-brown dorsum, red gills, no tail fin on 27 and 31 July) 38 and 42 days after hatching. One metamorph was deposited with the ANP museum.

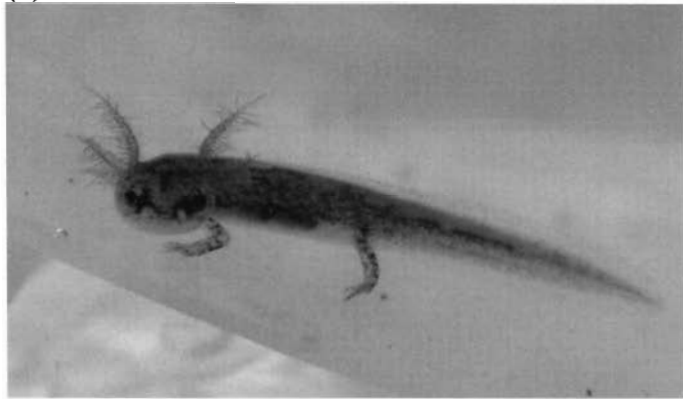
**Wild larvae.** I netted 10 wild *H. scutatum* larvae on 30 July, 2002 and 29 July, 2003 in an ANP wetland and 3 larvae on 27 June, 2004 and 22 July, 2004 in a DF wetland to observe and photograph larval development (Figures 1.2 a, b, c, d). Larvae moved little, infrequently swimming and settling to the bottom with legs extended. Mean  $\pm$  SD mm SVL of larval *H. scutatum* on 30 July, 2002 from Acadia National Park, Maine, was  $12.1 \pm 0.56$ , ( $n = 7$ ), and total length for larvae with uninjured tails was  $21.1 \pm 2.14$ , ( $n = 4$ ). Size (18 - 23 mm uninjured TL; 3 mm head width; 1 mm body width) indicated they were near metamorphosis (Blanchard 1923). A dark color surrounded the golden eyes that had round black pupils (Figures 1.2 a, b, c, d). A dark line crossed the eye and extended onto the face. Chin and throat were cream-colored, tapering off just past the

Figure 1.2. Larvae of *H. scutatum* in Maine: (a) newly hatched larva on 27 June 2004 (dorsal view); older larva on 22 July, 2004, (lateral (b) and dorsal (c) view); and older larvae on 30 July, 2003 (ventral view).

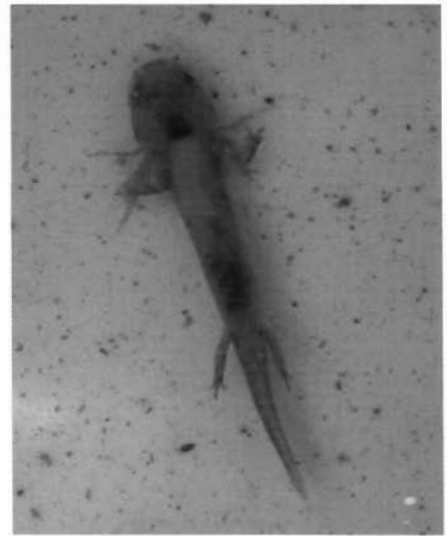
(a)



(b)



(d)



(c)

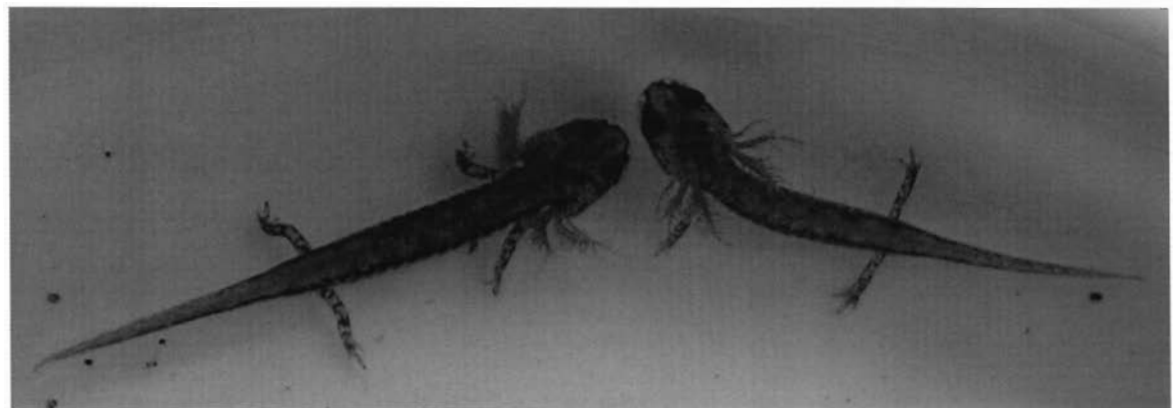
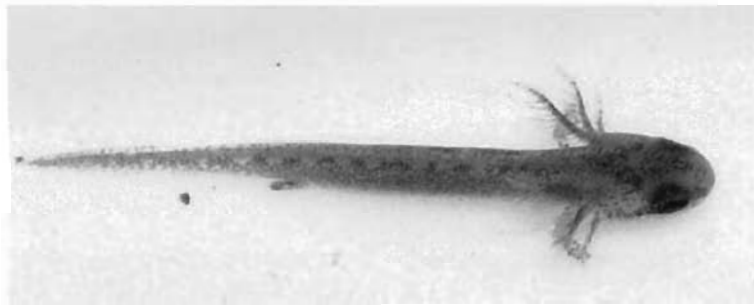


Figure 1.3. Comparison of *N. viridescens* larvae (a) and (d), 25 July, 2004 with *H. scutatum* larvae: (b) newly hatched, 27 June, 2004 and (c) near metamorphosis, 22 July, 2004, in Maine.

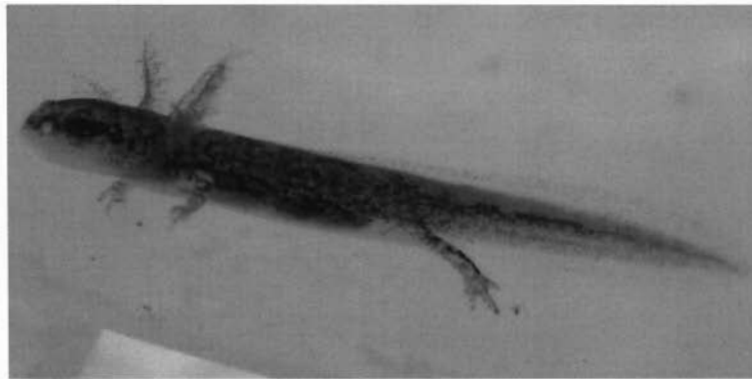
(a)



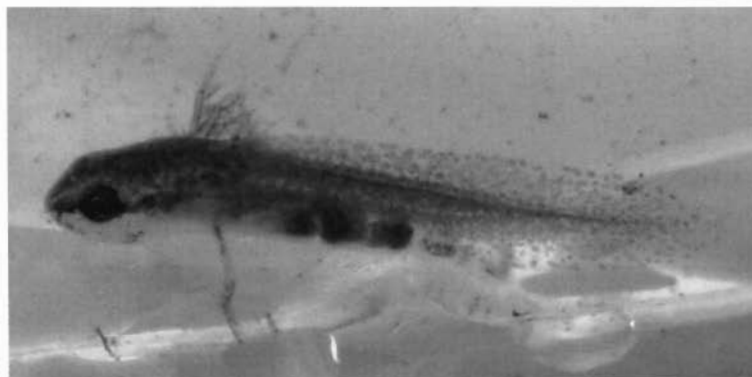
(b)



(c)



(d)



gills and front legs so that most of the salamander was dark on lateral view. The belly was no longer yellow. Gills were rust-colored, and this color extended down the back as a stripe on top of the rounded part of the tail under the fin. Larvae had a thin, clear, speckled top fin on the tail that no longer extended onto the body. Each foot had 4 toes. Larvae appeared exactly as drawn in Bishop (1941), closely resembled drawings in Parmelee et al. (2002), and resembled the coloration of drawings in Dodd (2003).

***Distinguishing *H. scutatum* from *N. viridescens* larvae.*** At total length < 18 mm, larvae of the 2 species resembled one another; both species were translucent, pale yellow-brown, without visible rear toes, and had a tail fin that extended onto the dorsal surface of the body (Figures 1.3). However, *H. scutatum* larvae could be distinguished by a dark Y shape mark on the head, dark dorsal mottles, and short toes on the front feet, unlike *N. viridescens* larvae (Figures 1.2 and Figures 1.3). A distinguishing feature when larvae were 18 - 23 mm in TL was the coloration: *N. viridescens* larvae continued to have yellow coloration and a tail with a tall, thin keel (Figures 1.3), while *H. scutatum* larvae had a ruddy dorsum, mottled dark sides, pale belly, patterned head, and had little or no keel on the tail (Figures 1.2 b, c, d and Figure 1.3 c). Also, on *H. scutatum*, the eyeline was present at and just beyond the eye, whereas on some *N. viridescens*, the eyeline extended into a stripe that extended to the tip of the tail. *N. viridescens* larvae were more active than *H. scutatum*, which were usually stationary except for occasional surfacing for air.

## DISCUSSION

Reliable survey methods are necessary for monitoring and studying *H. scutatum*. Population numbers seemed to be low, and the species was present in only 39% of wetlands searched. I found a maximum of 33 nests in a wetland, compared with 177 in Virginia (Harris, in press) and 68 in North Carolina (Corser and Dodd 2004). I found an average of 5.7 nests per wetland ( $n = 35$ ) and a mean of 4,774 m<sup>2</sup> per nest (i.e., 0.00137 nests per m<sup>2</sup>). In comparison, nest density in Tennessee is much higher, an average 13.3 nests ( $SD = 13.85$ ) per wetland ( $n = 11$ ) and a mean of 30 m<sup>2</sup> per nest (i.e., 0.020203 nests per m<sup>2</sup>), based on my calculations of Corser and Dodd's (2004) 5-year dataset.

The relation between species abundance and distribution strongly affects the sampling effort needed to assess species occurrence. *H. scutatum* are patchily distributed throughout their range, among wetlands, and along shoreline within a wetland. *H. scutatum* are rarely encountered in general amphibian surveys and, thus, specialized search efforts, or changes in existing methods, are needed to detect this species. Focusing surveys at appropriate seasons for the questions asked (e.g., population estimation, recruitment patterns, productivity) are of particular importance for infrequently encountered species. Searching for nests was the most successful method to locate *H. scutatum* in previously unsurveyed locations.

To monitor nesting populations, patch sampling, adaptive cluster sampling or percent area occupied techniques may prove useful, given the patchy distribution of the species (e.g., Smith 2003). This species is confined to discrete microhabitats during nesting (Chapter 2). Patches of this microhabitat can be visually identified initially (e.g.,

steep shoreline with a mean slope above the water surface of  $76.5^{\circ} \pm 14.9$  (Chapter 2), and then sampled in a random manner (Jaeger 1994).

### **Surveys of Adults on Roads During Rainy Spring Nights**

Searching for adult females on roads during rainy spring nights was useful to delineate migration routes, the start of nesting season, previously unknown populations, and potential breeding sites. Because of the paucity of salamanders in study areas and constraints of this method, few salamanders were observed. The maximum number of *H. scutatum* found with surveys of adults on roads during rainy spring nights was 4 salamanders and 10 tracks one night at Duck Brook Road, ANP. This count (14) is similar to the number of nests (16) subsequently found in adjacent wetlands. Constraints of this survey method include limited locations with minimal traffic on roads adjacent to breeding wetlands; a short period (1 - 4 nights) when conditions are suitable for migration; restriction of movement primarily to gravid females; and the unpredictability and regional variation of weather, which complicates scheduling these surveys.

This method would most efficiently be accomplished as part of a region-wide amphibian monitoring program in which many searchers were available to cover different areas simultaneously. Roads used for surveys should have minimal automobile traffic and be located near wetlands suitable for *H. scutatum* nesting. Observers would need to be familiar with the species and use bright lights with NiMh or lead acid batteries (e.g., night mountain biking lights, mining lamps, search light beams), because most observers were unable to detect this species when using only a 2-cell, D-battery flashlight. Observers also were unable to detect this species from a car, so walking along roads is required. Larger and more abundant species may be used as indicators of location and

time of *H. scutatum* migration (i.e., sub-surface, active *P. cinereus* or *A. maculatum*, *R. sylvatica*, and *P. crucifer* moving to mate and lay eggs). In Vermont, *A. laterale* were found migrating simultaneously with *H. scutatum* (J. Andrews, Middlebury College, personal communication).

### **Surveys of Nests**

I found the greatest number of *H. scutatum* by using nest surveys, which identified nesting habitat, enabled study of hatching success, and provided an opportunity to estimate success of metamorphosis related to length of hydroperiod. However, females may not breed every year (Harris and Ludwig 2004). I found nests from 27 April to 9 July. Nests occurred in relatively predictable, limited shoreline habitat adjacent to the deepest parts of the pool, along shoreline with steeper slope to water, and in vegetation that was deeper than along other parts of the shoreline (Chapter 2). A relatively long sampling window (41 - 70 days) existed in which to conduct the search, as compared to 1 - 4 nights for surveys of adults on roads during rainy spring nights.

*H. scutatum* is found in palustrine wetlands of a variety of vegetation and hydrologic classes, especially those with low flow, including streams dammed by beavers, marshes, swamps, vernal pools, and inlet areas of ponds. Bogs are one type of wetland in which this species was not found, and a negative relationship was obtained between *H. scutatum* presence and low pH and bog and fen vegetation (Chapter 2).

Within a wetland, nests are positioned above the water on steep shorelines, presumably so that as water levels decline during the lengthy embryo development, the aquatic larvae can drop directly into the water below when they hatch (*personal observation*, Harris in press, Richmond 1999). A search should concentrate on the part of

the shoreline that is at least a 60° angle from the water surface (Chapter 2). I searched the entire shoreline to find all available nest point locations, but this was time-consuming. Steep shoreline nest sites may be provided by wood, living vegetation, rock, or soil (Chapter 2). I found nests located in moss or accumulated litter from grasses, sedges, and ferns.

Novice searchers may mistake snail or slug eggs for unattended *H. scutatum* eggs, which can be differentiated by a clear outer jelly and distinct embryo, instead of opaque, rubbery texture of snail and slug eggs. *P. cinereus* eggs can be distinguished by their color (yellowish), absence of a thick layer of clear jelly, and the eggs are suspended from a stalk (Petranka 1998).

### **Dipnetting of Larvae**

The small (11 - 23 cm) larvae were difficult to detect with dipnets because of their small size, behavior, and coloration. Larvae were present during a 6-week period (16 June - 31 July). My surveys revealed distinguishing features between these species, especially during the period when *H. scutatum* were 18 - 23 mm TL. Metamorphosis of *H. scutatum* occurred when 23 mm TL was reached. Larval sampling provided information about approximate metamorphosis date and may be used to detect the presence of the species in a general amphibian survey, if conducted during the appropriate time in Maine. Larval netting is not an efficient way to detect new populations in Maine.

### **Incidental Pitfall Trapping Captures**

Pitfall trapping is a common method for surveying amphibian presence and abundance (Heyer et al. 1994). Researchers in the study area have deployed pitfall traps

to examine amphibian occurrence and dispersal. Kolozsvary (2003) recorded 15 captures of *H. scutatum* at 4 of 15 wetlands with 892 traps open during mid-June through September 2002 in ANP for an unspecified number of trap nights. Kolozsvary's (2003) traps were constructed from black plastic corrugated pipe with a 6 cm wide lengthwise opening cut in the top and sides consisting of deli containers; the traps were placed in the ground so that they surrounded 20% of the shoreline perimeter. C. Strojny (2004) captured 3 *H. scutatum* in 906 pitfall traps open 312 nights (282,672 trap nights) in PEF during 2002 and 2003. Strojny's (2004) traps were constructed from two #9 tin cans attached lengthwise and an inverted plastic funnel in the top can to inhibit escape; the traps were placed along drift fences (3 meters in length) in 99 plots distributed across 90 ha of upland forest. Brotherton et al. (in press) captured no *H. scutatum* in 49 traps open 27 nights (1,323 trap nights) in ANP during 2001. These traps included 17 pitfall traps constructed of two #9 tin cans and 32 minnow traps embedded sideways; traps were placed along 3 drift fence arrays in Sunken Heath, ANP.

Pitfall trapping may be inefficient for detecting new populations of *H. scutatum* in Maine because this method may entail a substantial commitment in time, money, and equipment to install and check traps (Heyer et al. 1994). Pitfall trapping can detect juveniles and adult age classes, depending on the location and time of trapping. Largest numbers would be expected when traps are deployed near breeding points during migration or dispersal. However, juvenile *H. scutatum* can climb out of traps, up the sides of glass containers, and over pitfall fencing (*personal observation*, David Patrick, University of Maine, personal communication). Installing pitfall traps and fencing around wetlands known to have *H. scutatum* (as detected by surveying for nests) could

provide information on total numbers of *H. scutatum* entering the wetland to nest and total numbers of young of the year exiting the wetland, to address questions such as dispersal distance and winter habitat of animals.

### **Visual Encounter**

Incidental observations of *H. scutatum* are rare in Maine, even among researchers studying amphibians. In my study area, 3 *H. scutatum* were seen by 30 University of Maine and Acadia National Park amphibian researchers and technicians during 1998 to 2003 during approximately 40,000 h of fieldwork in the study area. One *H. scutatum* was found in sphagnum at the edge of a pond in ANP (Brotherton et al., in press); 1 was found swimming in a wetland in ANP (J. Cunningham, University of Maine, unpub. data); and 1 was found in forest leaf litter in PEF (C. Strojny, University of Maine, unpub. data).

### **Recommendations for Surveying for *H. scutatum***

Targeted surveys are needed to detect new locations of *H. scutatum*, which are rarely encountered in general amphibian surveys. I recommend that surveys for nests be done during May and June in Maine. Characteristics of wetlands that should be searched include: pH > 5; water present during May, June, and July; and stable hydrology that does not flood during the nesting period. Searches should be concentrated along shorelines that have 1) slopes of 60 - 90°, 2) deep shoreline vegetation (11 cm), 3) deep water by shore (15 cm) and within 2 m from the shore (35 cm), 4) presence of moss, *C. canadensis*, *S. tomentosa*, *I. verticillata*, *Spiraea alba*, and *Onoclea sensibilis* along the shoreline, and 5) absence of *Kalmia angustifolia* and *C. calyculata* along the shoreline (Chapter 2). Because surveys for nests require parting shoreline vegetation, the

vegetation may tear and fall off steep shorelines, reducing available nesting habitat for *H. scutatum*. Vegetation disturbance can be minimized by training observers to be extremely careful parting vegetation and by restricting surveys of wetlands to every other year.

Detecting *H. scutatum* on roads during rainy spring nights provides the approximate date of the beginning of nesting season, after which surveys for nests may be conducted. Also, previously unknown locations of *H. scutatum* may be discovered. Observers should search simultaneously in several locations to increase the likelihood of detecting the species. Observers should be trained to look for the species, survey on foot (to better see this small species), use exceptionally bright lights (to better distinguish this species from twigs and worms on the road), and, search on warmer migration nights in winter or spring (e.g., after *A. maculatum* and *R. sylvatica* have first migrated).

Surveys for larvae should be conducted after most larvae have hatched and before larvae metamorphose. The start of the larval period can be determined by surveying for nests and observing when larvae hatch (16 June - 9 July in Maine). The end of the larval period occurs soon after larvae begin to develop adult coloration and reach a total length of approximately 18 - 23 mm (27 - 30 July in Maine). Researchers conducting larval amphibian surveys should become familiar with the identification and phenology of this species in order to detect *H. scutatum* larvae.

The landscape, wetland, and shoreline habitat used by nesting *H. scutatum* is presented in Chapter 2. The presence of *H. scutatum* in commonly used habitat types, however, does not mean the habitat necessarily supports a stable population of the species. All known nesting locations of this species and the surrounding uplands should

be monitored until it is known which wetland complexes support populations over the long term, especially given the apparent low numbers, scattered populations of the species, and tendency of females to skip years of reproduction (Harris and Ludwig 2004). This species was found in low numbers in most wetlands (median = 5 nests per wetland) and in 43% of randomly selected wetlands, suggesting that continued concern for this species is warranted in Maine.

Especially because of ongoing, dramatic declines in amphibian populations, it is important to begin monitoring this species. Long-term monitoring will provide information on the natural fluctuations of populations of this species, from which to observe any departures from the norm. Monitoring also will provide a measure of reassurance if species are continually present, even in the face of environmental changes. Ultimately, we need to halt the driving factors causing declines in amphibian population and range to allow amphibian populations to persist.

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**CHARACTERISTICS OF WETLANDS AND SHORELINE HABITAT USED BY  
FOUR-TOED SALAMANDERS (*Hemidactylium scutatum*)  
FOR NESTING**

**CHAPTER ABSTRACT**

I developed 3 logistic regression models with AIC<sub>c</sub> that predict the presence of four-toed salamander (*Hemidactylium scutatum*) nests at the wetland and shoreline point scales. I evaluated models with reserved data or jackknifing. First, I built a model predicting occupancy of a wetland by nesting *H. scutatum*, based on metrics describing the wetland and surrounding landscape collected at 35 wetlands containing *H. scutatum* nests and 32 wetlands in which nests were not detected. Wetlands with nests were best distinguished from those without nests by having higher pH ( $\bar{x} = 5.5$ ) and less frequently being shrub scrub (31%) or unconsolidated bottom (6%) National Wetland Inventory classes. Second, I predicted location of nests along the shoreline of wetlands, with data collected at nests ( $n = 239$ ) and at randomly selected, unoccupied shoreline points ( $n = 294$ ) within occupied wetlands. The best model correctly classified 83% of reserved data: Shoreline points with nests had steeper shores ( $\bar{x} = 76.5^\circ$ ), greater near-shore ( $\bar{x} = 14.2$ ) and basin water depth (cm) ( $\bar{x} = 31.9$ ), deeper (cm) shoreline nesting vegetation ( $\bar{x} = 11.4$ ), and more frequent presence of moss (98%) and winterberry (*Ilex verticillata*) (58%) within 1 m of shoreline points. Shoreline points with nests less frequently were associated with leatherleaf (*Chamaedaphne calyculata*) (6%), meadowsweet (*Spiraea alba*) (12%), and

*Kalmia angustifolia* (2%) within 1 m. Third, I built a model predicting *H. scutatum* nesting at wetlands, based on shoreline point data collected at randomly-selected, unoccupied shoreline points ( $n = 294$  from occupied wetlands and  $n = 258$  from unoccupied wetlands). The best model correctly classified 67% of reserved data: shoreline available in wetlands with nests more frequently had *Sphagnum* spp. available for egg attachment (82%), woody debris substrate (46%), flow of water (26%), and, within 1 m of shoreline points, the presence of blue joint reed grass (*Calamagrostis canadensis*) (29%), *S. alba* (12%), steplebush (*Spiraea tomentosa*) (17%), and sensitive fern (*Onoclea sensibilis*) (7%). Shoreline in occupied wetlands less frequently had sheep laurel (*K. angustifolia*) (2%) within 1 m and deciduous forest class (17%) within 5 m of shoreline points. The habitat models I present provide information on microhabitat, wetland habitat, and surrounding upland habitat that *H. scutatum* occupies. The definitions of nesting habitat I present will assist land managers and researchers in detecting wetlands with nests of *H. scutatum*, detecting nests within wetlands, enabling implementation of a monitoring program for this species, and providing guidance for the protection and management of *H. scutatum*.

## INTRODUCTION

Conservation planning for the four-toed salamander (*Hemidactylium scutatum*) may be warranted given global declines in population, health, and range of many amphibian species (reviewed by Berger et al. 1999, Blaustein and Johnson 2003, Chalmers 1998, Ferraro and Burgin 1993, Houlahan 2000, Young et al. 2001) and wetland destruction and isolation potentially affecting reproductive success (Gibbs 1993,

2000, Guerry 2000, Wilen and Frayer 1990). The four-toed salamander (*Hemidactylium scutatum*) is listed as *Special Concern* in Maine and 11 additional states and provinces, *Threatened* in Illinois, and *Endangered* in Indiana (Appendix A). The species' occurrence is patchy (Petranka 1998). An undetermined number of individuals of this species have been recorded in 32 "sites" in Maine (P. deMaynadier, Maine Department of Inland Fisheries and Wildlife, *personal communication*).

Amphibians have a complex life cycle with variation in morphology and resource use among life phases (Moran 1994). To adequately protect habitat, amphibian use of habitat during a variety of life phases must be understood. Habitat use by a species (i.e., *H. scutatum*) with a complex life cycle and presumably small home range, is strongly affected by adjacent habitat available for other life phases.

Modeling is a useful technique to reduce many habitat variables to a few and to relate the variables with various aspects of a species' ecology. Models may be developed to predict species occurrence and elucidate important biological variables and relationships between a species and the environment (Austin 2002). Insights learned in developing predictive models will improve the ability to evaluate potentially suitable habitat. An improved ability to evaluate potentially suitable habitat will provide guidance for surveys of the species and for identifying types of habitat to be managed or conserved.

Understanding the modeling process is requisite to comprehending and interpreting results. The species-environment modeling process is described by Guisan and Zimmermann (2000) as (1) model formulation (i.e., based on ecological theory and exhibiting two possible strengths of generality, reality or precision), (2) design of data

collection, (3) statistical model formulation (e.g., exploratory and model building), (4) model calibration, (5) prediction; (6) model evaluation (i.e., validation or accuracy assessment), and (7) model credibility and applicability. Models may be complex, including multiple resource-partitioning gradients that affect multiple life phases of a species. These multivariate habitat models can be compared with Akaike Information Criterion (AIC, Burnham and Anderson 2002) to test a variety of alternative hypotheses.

Use of habitat at the macrohabitat scale and the microhabitat scale is influenced by food type, food size, diel time, and seasonal time (Schoener 1974) as well as colonist availability, point fidelity, learned behavior, competition, and predators. Environmental predictors that describe habitat suitability can be categorized as “resource” gradients (e.g., water) consumed by the organism, “direct” gradients (e.g., temperature, pH) with direct influence on the physiology of the organism, and “indirect” gradients (e.g., slope, aspect, topographic position, geology, habitat type) that indirectly affect the organism (Austin 2002). Indirect gradients typically are used in habitat-occupancy models because they may replace a combination of resources and the direct gradients in a simple way, and they are more easily measured (Guisan and Zimmermann 2000). Gradients can be grouped into categories based on their affect on the species or particular life phase. If reliable and accurate measurements of all environmental gradients important to the species are measured at temporal and spatial scales relevant to the species (Conroy and Moore 2002), most important biological effects should be identified in the statistical model developed.

*H. scutatum* adults are lungless (Family Plethodontidae) invertivores that nest in wetlands and reside under forest debris during the non-nesting season (Petranka 1998),

although little is known of adult habitat use and ecology. Breeding occurs in late summer through fall (Bishop 1941), and females migrate to wetlands in spring (or winter in their southern range) to lay eggs in wetland shoreline vegetation, typically *Sphagnum* spp. (Harris in press). Nests may contain eggs from more than one female, but, typically, only one female will brood the eggs until hatching (Petranka 1998). Females may not breed every year (Harris and Ludwig 2004). Larvae are aquatic, carnivorous, and cryptic (Petranka 1998). It is not known when juveniles migrate to uplands or where they overwinter, and little is known of juvenile ecology.

The species' population status is unknown in most of its range because *H. scutatum* are seldom encountered opportunistically, observers do not know how to reliably or efficiently locate new populations of the species (but see Chapter 1), and *H. scutatum* are patchily distributed (Petranka 1998). To enhance populations of this species, it is important to know what type of wetlands this species uses for reproduction and to conserve those wetlands. Also, because surveying for nests is an effective method of surveying this species (Chapter 1), my characterization of nest habitat will increase the ability of observers to detect the species in previously unknown populations and thus begin monitoring nesting populations of *H. scutatum*.

I examined *H. scutatum* use of wetlands and shoreline points for nesting, which occurs during a discrete seasonal period when attendant females are sedentary (*personal observation*) and do not eat (Wood 1953, Harris in press). My objective was to model *H. scutatum* habitat selection at the scale of the wetland and the scale of the nest point to identify important biological habitat variables associated with nesting *H. scutatum* in Maine. *H. scutatum* will most frequently be present in wetlands that are suitable for egg

and larval development (e.g., wetland type, water chemistry) and have appropriate surrounding terrestrial environment for juveniles and adults (e.g., forest type, connectivity, density of wetlands nearby). Females may select shoreline points within a wetland that are suitable for attendant females and egg development (e.g., microclimate, risk of being preyed upon, risk of flooding) and that facilitate hatching and dropping directly into water (Harris in press).

I surveyed 67 Maine wetlands for nesting *H. scutatum* and identified occupied and unoccupied habitat at the wetland- and nest-point scale. I collected data on environmental variables and combined the variables into different logistic regression equations (i.e., models). I compared the logistic regression models with AIC<sub>c</sub> to select the best model and the most important predictor variables. I built 3 models. First, I built a predictive model of wetlands with nesting *H. scutatum* with metrics describing the wetland and surrounding landscape. Second, I predicted nest point location along the shoreline of wetlands, with data collected at nests and at randomly selected, unoccupied points within the same wetland. Finally, I built a model predicting wetlands that would contain nesting *H. scutatum* with nest scale data collected at randomly selected, unoccupied points from wetlands with and without nests. The models based on shoreline point data enabled me to study selection of shoreline points for nesting in wetlands in which the species (and therefore also the appropriate habitat) was present as well as to determine whether shoreline habitat in wetlands with nests differed from that in wetlands without nests.

## **METHODS**

### **Study Area**

I surveyed wetlands in coastal and southern Maine in Acadia National Park (ANP), University of Maine Demeritt Forest (DF), University of Maine Foundation Penobscot Experimental Forest (PEF), USDA Forest Service Northeastern Research Station Massabesic Experimental Forest (MEF), and USFWS Sunkhaze Meadows National Wildlife Refuge (SMNWR). I describe the study areas and historical records for *H. scutatum* in the study areas in Chapter 1.

### **Survey Method**

I conducted complete, timed surveys for nesting *H. scutatum* in 67 wetlands on the 5 study units. I surveyed 30 wetlands in ANP during 27 April - 21 June, 2002, and I surveyed 37 wetlands [ANP ( $n = 12$ ), MEF ( $n = 16$ ), PEF ( $n = 4$ ), DF ( $n = 3$ ), and SMNWR ( $n = 2$ )] during 23 April - 24 June, 2003. My survey method is described in Chapter 1.

### **Wetland Measurements**

Wetland metrics were measured once at each wetland and included stream presence, water chemistry, dominant National Wetland Inventory class of the wetland (NWI; Cowardin et al. 1979), and 2 measures of the surrounding landscape (Table 2.1). Stream presence may provide a longer hydroperiod, greater nutrient input, and an increased likelihood of fish presence and risk of flooding. Water chemistry affects larval physiology (Pierce 1985) and will influence the available prey community. Characteristics of the surrounding landscape may affect colonization rates and survival for juveniles and adults. I obtained landscape metrics, using GIS, of the percent of

dominant, upland forest class and the percent wetland area occurring within 200 m buffers around wetlands (Table 2.1). I selected a 200 m buffer because it was larger than the home range ( $24 \text{ m}^2$  for females; Petranka 1998) of the similar-sized, terrestrial, red-backed salamander (*Plethodon cinereus*) and smaller than the farthest distance (467 m, K. Montieth, University of Rhode Island, personal communication) traveled by the larger, wetland-breeding spotted salamander (*Ambystoma maculatum*). I calculated the search area with GIS and I recorded search times. I opportunistically recorded presence of beaver (e.g., dams, gnawed trees) and fish, but did not include these data in model development.

### **Measurements of Shoreline Points With and Without Nests**

I measured habitat variables at 239 nests and I measured the same variables at randomly-selected, unoccupied shoreline points ( $n = 294$  among 35 occupied wetlands and  $n = 258$  among 32 unoccupied wetlands) (Table 2.2). I measured variables once at each nest or unoccupied shoreline point [hereafter collectively termed ‘shoreline points’]. To select unoccupied shoreline points, I used a random number table to select a compass direction and distance to travel to reach a  $10 \text{ cm}^2$  area along the shoreline, which I carefully searched. If no *H. scutatum* were present, I measured the shoreline point as if it were a nest. I measured a minimum of 8 shoreline points per wetland without nests, and if there were  $> 8$  nests, I measured an equal number of occupied and unoccupied shoreline points. To select unoccupied shoreline points, I defined ‘shoreline’ as vegetation or mineral matter with sufficient structural support to hold a golf ball (i.e., approximating the volume of a typical *H. scutatum* nest and approximating the structural support typically found at nests, which were able to support the weight of a golf ball).

Table 2.1. Variables measured at 67 Maine wetlands and surrounding 200 m buffers, 2002 and 2003.

Variable	Data range	Equipment	Life stage affected
<b>Wetland</b>			
pH	4.0 to 6.7	YSI 60 <sup>a</sup>	larvae
Specific conductance $\mu\text{S}/\text{cm}$	13.3 to 426.7 <sup>b</sup>	YSI 85 <sup>a</sup>	larvae
Clarity <sup>c</sup> PCU	3 to 328	Spectrophotometer	larvae
ANC <sup>d</sup> ( $\mu\text{eq}/\text{L}$ )	-30.88 to 317.04	Gran titration	larvae
NWI wetland class	FO1, FO4, FO5, SS, EM, AB, UB, ML <sup>e</sup>	GIS	adult, eggs, larvae
Stream	presence, absence	GIS	adult, eggs, larvae
<b>Buffer, 200m around wetland</b>			
Wetland area	0-100% wetland area over 200 m buffer	GIS	adult, juvenile
Upland forest	mixed, conifer, deciduous dominant in 200m buffer	GIS	adult, juvenile

<sup>a</sup> YSI 60 and 85, Yellow Springs Instruments, Yellow Springs, Ohio.

<sup>b</sup> highest value within 10 m of road at site ID 394 in ANP.

<sup>c</sup> Clarity (Percent Color Unit) was measured in Acadia National Park wetlands only.

<sup>d</sup> ANC (Acid Neutralizing Capacity) was measured in Acadia National Park wetlands only.

<sup>e</sup> Cowardin et al. (1979) classification of tallest vegetation covering at least 30% of wetland (FO1 = deciduous forest, FO4 = coniferous forest, FO5 = dead forest, SS = shrub scrub, EM = emergent, AB = aquatic floating bed, UB = unconsolidated bottom (no vegetation), and ML = moss-lichen).

Table 2.2. Variables measured at *H. scutatum* nests and randomly selected, unoccupied shoreline points in 35 wetlands with nests and 32 wetlands without nests in Maine, 2002 and 2003.

Variables	Range or category of data	Life stage affected
<b>Micro-climate</b>		
Relative humidity in shore	90.4-99.9%	eggs, adult
Relative humidity of air	40.0-99.9%	eggs, adult
Temperature in shore vegetation <sup>a</sup>	5-32 °C	eggs, adult
Temperature of air	5-32 °C	eggs, adult
Temperature of water	4-27 °C	eggs, adult, larvae
Canopy cover 10 cm above shore	0-25%, 25-50%, 50-75%, 75-100%	eggs, adult, larvae
Aspect of shore	N, NE, E, SE, S, SW, W, NW	eggs, adult, larvae
<b>Hydrology</b>		
Water depth at shore <sup>a</sup>	0-110 cm	larvae
Maximum depth of water within 2 m	0-250 cm	larvae
Slope of basin <sup>a</sup>	0-90°	larvae
Water flow <sup>a</sup>	0, present	eggs, adult, larvae
<b>Structure</b>		
Substrate under shore <sup>a</sup>	wood, living vegetation, rock, soil	eggs, adult, larvae
Slope from water to shore <sup>a</sup>	0-90°	eggs, adult, larvae
Depth of shoreline vegetation <sup>a</sup>	0-32 cm	eggs, adult
Material eggs attached to <sup>a</sup>	<i>Sphagnum</i> , other moss, non-moss	eggs, adult
<b>Associated Vegetation</b>		
Plants within 10 cm <sup>2</sup> of shoreline	0-6 of 88 total species	eggs, adult
Plants within 1 m <sup>2</sup> <sup>a</sup> of shoreline	0-10 of 115 total species	eggs, adult, larvae
Vegetation class in 5 m <sup>2</sup> <sup>a</sup> of shoreline	FO1 <sup>b</sup> , FO4, FO5, SS, EM, AB, UB, ML	eggs, adult, larvae

<sup>a</sup> Variable selected during exploratory analysis to use in model building.

<sup>b</sup> Cowardin et al. (1979) classification of wetlands, based on tallest vegetation class covering at least 30% of wetland (FO1 = deciduous forest, FO4 = coniferous forest, FO5 = dead forest, SS = shrub scrub, EM = emergent, AB = aquatic floating bed, UB = unconsolidated bottom (no vegetation), and ML = moss-lichen).

For shoreline to be occupied by a nest, the microclimate must be suitable for eggs and female attendants. I described shoreline points with the metrics: temperature of air and nest, relative humidity of air and nest, canopy cover, and aspect (Table 2.2). Canopy cover and aspect influence temperature and thus moisture. I measured percent canopy cover with a mirror placed directly over the shoreline point vegetation but under any understory vegetation (e.g., ferns). I measured aspect with a compass and measured relative humidity with a calibrated meter. I measured temperature of air with a thermometer shaded from direct sunlight and located 10 cm above a shoreline point. I measured temperature of shoreline points with a thermometer inserted into shoreline vegetation parallel to the outer surface of the vegetation so that the temperature was consistent along the length of the probe.

Occupancy of a shoreline point also may depend on the suitability for larvae of the surrounding aquatic environment, which may remain < 1 m from nests (Harris et al. 2003). Persistence of water is critical to larval metamorphosis, and females appeared to lay eggs near deeper water (*personal observation*, Richmond 1999). Wetland-breeding amphibians are typically constrained by availability of wetlands with a sufficiently long hydroperiod persisting from egg-laying through metamorphosis that simultaneously contain few fish (Toft 1985, Wilbur 1980), which eat *H. scutatum* larvae (Kats 1988). In Maine, the larval period of *H. scutatum* occurs from June 16 to July 30 (Chapter 1). I thus measured variables that relate to hydroperiod (e.g., temperature of water, water depth under shoreline point, maximum water depth within 2 m of shoreline point, slope of basin, presence of flowing water) (Table 2.2). I measured depth of water under shoreline points to determine if females laid eggs by water deeper than the water at

unoccupied shoreline points. I measured maximum depth of water occurring within 2 m of shoreline points (i.e., likely the deepest area to which larvae could retreat as surface water area decreases during June - August). I measured slope of the shoreline from the water surface and slope of the basin under shoreline points, because a shallow basin slope indicates a greater likelihood of hatching larvae having to drop onto dry shore, necessitating overland travel to water. I recorded presence of flowing water, defined as any perceptible horizontal flow of water (e.g., not including springs with only vertical flow in water column). Flowing water may indicate a portion of a wetland with longer hydroperiod, greater nutrients, a greater likelihood of fish presence and a greater risk of flooding.

Temporary wetland communities are complex systems in which temperature interacts with hydrology, predators, competitors, kin selection, size of larvae, and community composition to affect larval growth, time of metamorphosis, and use of habitat. Higher temperatures are correlated with an increased risk that embryos and larvae will desiccate, because water evaporates more rapidly at higher temperatures. Decreasing wetland surface area from drying also may increase the rate at which larvae are preyed upon because larvae are concentrated in remaining pools, although some anuran larvae can avoid drying by increasing the rate of development (Denver et al. 1998). Higher surface temperature may be correlated with open vegetation. Water temperature, water source, and nutrients of a wetland may be related (e.g., groundwater-fed wetlands have lower water temperatures, wetlands with little canopy cover have higher water temperature related to greater amounts of sunlight, which may produce more nutrients through photosynthesis).

Temperature directly influences amphibian physiology, notably by increasing the rate of egg and larval development and growth rate with warming (Rome et al. 1992). Rapid development to a larger size may benefit larvae through decreased risk of being preyed on by interspecific larvae. Larval size likely does not confer a competitive advantage in foraging as long as prey is small relative to gape size (Smith 1990). Rapid development increases the chance of metamorphosis before wetlands seasonally dry and enhances survival to maturity, earlier maturity, and larger size and fecundity at maturity (Semlitsch and Gibbons 1990, Wilbur 1997). The benefits of rapid development to a larger size may be offset by the costs of foraging activity, which increase risk from predators. These foraging-activity tradeoffs are mediated by habitat, food location, temperature, and kin-selection behavior (Harris et al. 2003, Holomuski 1986, Kats et al. 1988, Wellborn et al. 1996). The benefits of large embryos resulting in large larvae may be transient (Semlitsch and Gibbons 1990) or negated by higher rates of predation on larvae, which may develop proportionately shorter tails in warmer water (Kaplan 1992).

I measured temperature of water with a thermometer shaded from direct sunlight and placed horizontally near the surface of the water next to shoreline points. I did not record hydroperiod of wetlands, but provide approximate dates of *H. scutatum* metamorphosis (Chapter 1).

Finally, I described vegetation structure (i.e., substrate type, shoreline vegetation dimensions, nest placement relative to water), and associated plant species (e.g., which may indicate local hydrology, climate, and structure) (Table 2.2). Plants create habitat structure for *H. scutatum* nests by supporting nests above water, which thereby reduces flooding threat and facilitates hatching into water; retaining moisture; and by providing

nest concealment (Table 2.2). Nest support was provided by substrate that I categorized as wood, living vegetation, soil, or rock (Table 2.2). Plants also indicate current and historical environmental conditions. The presence of a particular plant species in a wetland can be a sensitive indicator of the aquatic habitat (Tiner 1999) and thus may indicate suitability of the habitat for salamander nests and larvae. I recorded the type of vegetation to which eggs were attached, the dominant plant species occurring within 10 cm and 1 m of each nest, and the dominant vegetation structure (with the NWI classification system) within 10 m (Table 2.2).

## ANALYSES

I used logistic regression, a general linear model appropriate for presence/absence data, to develop models of *H. scutatum* selection of wetland and nest point habitat. I developed a suite of models for each of 3 analyses: predicting wetlands with nests, shoreline points with nests within these wetlands, and shoreline point characteristics that differ between wetlands with nests and those that are unoccupied. Models were ranked with Akaike Information Criterion for small sample size (AIC<sub>c</sub>, Burnham and Anderson 2002). Shoreline point models were randomly partitioned *a priori* for exploratory analysis and variable reduction (25%), model building (50%), and data reserved to evaluate the best model (25%). The best wetland model was evaluated with jackknifing. I conducted all statistical analyses with Systat 10.2a (SYSTAT Software Inc, 2002), except for jackknifing, which I conducted with S-PLUS 6.1 (Insightful Corp., 2002).

## **Reduction of Variables for Shoreline Point Analyses**

I reduced the candidate set of predictor variables (Table 2.2) during exploratory analysis. I retained variables if the univariate logistic regression  $P$ -value was  $< 0.2$  or if it was in the best exploratory logistic regression model as assessed by  $AIC_c$  comparisons. Several plant species that seemed to indicate nesting presence based on field observations also were retained. Variables were tested for correlation with Pearson correlation coefficients and one of the correlated variables was excluded during exploratory analysis in most cases. Correlated plant species variables that were equally useful as predictors were retained for the model building process, at which point the less useful predictor variable was identified and eliminated.

## **Development of Models for Shoreline Point Analyses**

Models included the best models developed during exploratory analysis, models representing field experience, and models built by manual and automated forward stepwise regression. After evaluating the merits of including only *a priori* models (those based only on exploratory analysis and field experience intuition) versus models selected during the model-building process, I decided to include the latter models. The rationale was that this is largely an exploratory study with rigorous evaluation protocol. Although overfitting of the data is possible with inclusion of models selected by automated logistic stepwise regression, this will be offset by model evaluation.

## **Ranking and Selecting Models**

I compared models with relative Kullback-Leibler information (Kullback and Leibler 1951) with  $AIC_c$  to identify the most parsimonious logistic models that discriminated between occupied and unoccupied wetlands and shoreline points. I tested

global and best-fit models for goodness-of-fit with Hosmer-Lemeshow statistics ( $P > 0.10$ ) (Anderson and Burnham 2002). In addition to  $AIC_c$ , I calculated differences from the best model ( $\Delta AIC_c$ ), Akaike Weights for each model, and I ranked variables by their importance (Burnham and Anderson 2002).

### **Evaluation of Models for Wetland Analyses**

I jackknifed the best-supported model and present the results in terms of  $\Delta AIC$ .

### **Evaluation of Models for Shoreline Point Analyses**

I conducted evaluations of model reliability with independent, reserved data based on percent correct classification. I used the typical threshold levels for classification of  $< 0.5$  (model predicts absence correctly),  $= 0.5$  (model prediction is substantially similar to random), and  $> 0.5$  (model predicts presence correctly). Choice of the cutoff point is analogous to decisions regarding Type I and II errors (Zabel et al. 2002).

## **RESULTS**

I found 238 *H. scutatum* nests in 35 (52.2%) of 67 wetlands I searched and 24 (43%) of 56 of randomly selected wetlands contained *H. scutatum* nests. Detection of salamander nests was not related to the duration of the search ( $n = 67$ ;  $P = 0.127$ ;  $t = 1.526$ ). I calculated a mean of  $5.7 \pm 5.7$  SD nests per wetland, and the most nests I found in a wetland was 33. Nest density is presented in Chapter 1.

### **Models to Predict *H. scutatum* Occupancy of Wetlands**

To develop the best model to predict a wetland that contains *H. scutatum* nests, I used variables in different combinations to create 25 logistic regression equations (i.e., models). I calculated candidate models and ranked them with  $AIC_c$  (Table 2.3). The best

Table 2.3. Candidate models for predicting wetland occupancy by *H. scutatum* nests, with data from 67 Maine wetlands, 2002-2003 and evaluated by Akaike's Information Criterion for small samples ( $AIC_c$ ).

MODEL ID#	pH	Specific conductance	FO1 NWI class	SS NWI class	EM NWI class	UB NWI class	FO4 NWI class	AB NWI class	Wetland density in 200m buffer	Conifer dominant in buffer	Deciduous dominant in buffer	Mixed dominant in buffer	Stream connectivity	K	Deciles of Risk	Log Likelihood	$AIC_c$	change in $AIC_c$	L (g data)	Akaike Weight
14	x			x		x								5	0.759	-32.801	76.586	0.000	1.00020	0.267
23	x			x										4	0.326	-34.677	77.999	1.413	0.49333	0.132
1	x													3	0.007	-35.855	78.091	1.505	0.47120	0.126
18	x					x								4	0.403	-34.976	78.597	2.011	0.36583	0.098
19	x												x	4	0.403	-35.094	78.833	2.247	0.32511	0.087
15	x			x		x							x	6	0.72	-32.887	79.174	2.588	0.27417	0.073
24	x		x											4	0.175	-35.532	79.709	3.123	0.20980	0.056
17	x					x							x	5	0.527	-34.544	80.072	3.486	0.17503	0.047
21	x								x				x	5	0.085	-34.553	80.090	3.504	0.17346	0.046
25	x											x		4	0.16	-35.816	80.277	3.691	0.15793	0.042
20	x				x								x	5	0.371	-35.092	81.168	4.582	0.10119	0.027
13													x	3		-43.093	92.567	15.981	0.00034	0.000
22				x		x							x	5		-41.304	93.592	17.006	0.00020	0.000
6						x								3		-44.416	95.213	18.627	0.00009	0.000
8								x						3		-45.047	96.475	19.889	0.00005	0.000
2		x												3		-45.168	96.717	20.131	0.00004	0.000
11											x			3		-45.717	97.815	21.229	0.00002	0.000
4				x										3		-45.83	98.041	21.455	0.00002	0.000
5					x									3		-45.931	98.243	21.657	0.00002	0.000
7							x							3		-46.027	98.435	21.849	0.00002	0.000
9									x					3		-46.117	98.615	22.029	0.00002	0.000
3			x											3		-46.264	98.909	22.323	0.00001	0.000
12												x		3		-46.365	99.111	22.525	0.00001	0.000
10										x				3		-46.373	99.127	22.541	0.00001	0.000
16	x	x	x	x	x	x	x	x	x	x	x	x	x	15	0.382	-30.063	99.538	22.952	0.00001	0.000

models are those that best approximate the data and are indicated by large Akaike Weights (Burnham and Anderson 2002). The most parsimonious model included pH and shrub scrub and unconsolidated bottom NWI classes (Table 2.3). The variable, stream presence, appeared in several of the models that were less supported (Table 2.3). I ranked variables by importance by summing the Akaike Weight from all models that included the variable (Burnham and Anderson 2002). Variables with summed Akaike Weights > 0.2 are presented in Table 2.4. Jackknifing the best-supported model resulted in an average  $\Delta$  AIC value of 4.13 (range = 0 - 5.144), within the range of the top 10 models (Table 2.3).

Wetlands with nesting *H. scutatum* had higher average pH than wetlands without nests (Table 2.4). Occupied wetlands were less likely to be classified as shrub scrub (11 wetlands) than unoccupied wetlands (14 wetlands) and were less likely to be classified as unconsolidated bottom (2 occupied wetlands versus 7 unoccupied wetlands, Table 2.4). Occurrence of streams was positively associated with the presence of *H. scutatum* in wetlands and occurred more frequently in occupied ( $n = 25$  wetlands) than unoccupied ( $n = 13$  wetlands) wetlands (Table 2.4). Wetlands with and without nesting *H. scutatum* are shown in Figures 2.1 and 2.2.

### **Models to Predict Locations of *H. scutatum* Nests Along Shoreline**

I compared nests with randomly selected, unoccupied locations within wetlands that contained nests. I partitioned data into 3 sets for exploratory analysis ( $n = 134$  points; 56 points with nests and 78 points without nests), model building ( $n = 238$  points; 94 points with nests, 144 points without nests), and evaluation ( $n = 120$  points; 48 points with nests, 72 points without nests). In exploratory analysis, I retained most shoreline

Table 2.4. Variables best predicting wetland occupancy by *H. scutatum* nests, based on 67 wetlands in Maine, 2002-2003.

Variable	Importance ranking of variable <sup>a</sup>	Logistic regression parameters from best model		Descriptive data for important variables					
				Wetlands with nests			Unoccupied wetlands		
		$\beta$	<i>SE</i>	$\bar{x}$	<i>SD</i>	Range or sum	$\bar{x}$	<i>SD</i>	Range or sum
pH	0.99	+2.164	0.576	5.57	0.53	4.17-6.71	4.91	0.54	4.19-6.23
UB class	0.48	-1.814	1.085	6%	24%	2	22%	42%	7
SS class	0.47	-1.275	0.660	31%	47%	11	44%	50%	14
Stream presence <sup>b</sup>	0.28			71%	46%	25	41%	50%	13

<sup>a</sup> Sum of Akaike Weights for models containing the variable (Burnham and Anderson 2002); see table 2.3 for weights.

<sup>b</sup> Variable of stream presence not in most parsimonious model, thus, no logistic regression parameter applicable.

Figure 2.1. Example photos of wetlands in which *H. scutatum* were present.



Figure 2.2. Example photos of wetlands in which *H. scutatum* were absent.



point variables describing the basin and shoreline during model-building (Table 2.2).

Variables I omitted include: all plant species occurring within 10 cm of shoreline points, 103 plant species recorded within 1 m of shoreline points, and most variables relating to climate (Table 2.2). I discontinued relative humidity measurements because shoreline relative humidity was usually 99% at nests and shoreline points without nests. I calculated and ranked 40 logistic regression models with AIC<sub>c</sub> (Table 2.5).

The best-supported models are indicated by large Akaike Weights in the far right column of Table 2.5. I ranked variable importance, and variables with summed Akaike Weights > 0.3 are presented with their descriptive data in Table 2.6. The direction of effect of variables included in the best-supported model are indicated by ( $\beta$ ) in Table 2.6.

Shoreline containing *H. scutatum* nests had deeper nesting vegetation, deeper water under the nest, deeper water within 2 m, a positive association with moss and winterberry (*Ilex verticillata*), and negative associations with meadowsweet (*Spiraea alba*), leatherleaf (*Chamaedaphne calyculata*), and sheep laurel (*Kalmia angustifolia*), compared to shoreline points without nests (Tables 2.5 and 2.6). The best logistic regression models for nest presence (Table 2.5) were used to classify an independent data set. The model correctly classified 100 (83%) of 120 points (Table 2.7). Shoreline with and without *H. scutatum* nests is shown in Figures 2.3 and 2.4.

### **Models to Predict *H. scutatum* Occupancy of Wetlands Based on Available, Unoccupied Shoreline Points at Wetlands With and Without Nests**

I distinguished shoreline point characteristics between wetlands with and without nests. I randomly partitioned data *a priori* into 3 sets for exploratory analysis ( $n = 130$ ; 78 from wetlands with nests, 52 from wetlands without nests), model building ( $n = 275$ ; 144 from

Figure 2.3. Example photos of shoreline with *H. scutatum* nests.



Figure 2.4. Example photos of shoreline without *H. scutatum* nests in wetlands with the species.



Table 2.5. Candidate models to predict *H. scutatum* nest points along the shoreline of wetlands with nests, based on data ( $n = 219$ ) from 35 Maine wetlands with nests and evaluated with Akaike's Information Criterion for small samples (AIC<sub>c</sub>), 2002-2003.

MODEL ID#	C										Hydrology				Associated Plant Species (1m)										Deciles of Risk	log likelihood	AIC <sub>c</sub>	change AIC <sub>c</sub>	W <sub>i</sub>					
	Nest temperature	Structure					Hydrology				Associated Plant Species (1m)																							
	depth nesting vegetation	substrate alive	substrate wood	substrate soil	NWI emergent	NWI shrub scrub	NWI FO1	NWI FO4	Slope	eggs attach sphagnum	eggs attach any moss	h2O depth under nest	dist.until water deeper	maximum water depth	flow	sphagnum	any moss	moss not sphagnum	<i>Calamagrostis canadensis</i>	leaf litter	<i>Alnus</i>	<i>Spirea latifolia</i>	<i>Spirea tomentosa</i>	<i>Ilex verticillata</i>	<i>Kalmia angustifolia</i>	<i>Onoclea sensibilis</i>	<i>Osmunda cinnamomea</i>	<i>Acer rubrum</i>	<i>Vaccinium angustifolia</i>	<i>Chamaedaphne calyculata</i>				
31		X						X	X			X		X		X						X	X	X				X	12	0.518	-78.071	181.657	0.000	0.373
35	X	X						X	X			X		X		X						X	X	X				X	13	0.612	-77.642	183.06	1.403	0.185
39		X			X				X			X		X		X						X	X	X				X	13	0.359	-77.835	183.446	1.789	0.152
38		X						X	X			X		X								X	X					X	11	0.447	-80.137	183.549	1.893	0.145
36	X	X						X	X			X		X	X	X						X		X			X	X	14	0.469	-77.352	184.763	3.106	0.079
32		X					X		X			X		X		X							X	X			X		11	0.076	-81.739	186.753	5.097	0.029
22		X						X	X			X		X		X						X	X	X					11	0.233	-81.814	186.903	5.247	0.027
25		X					X		X			X		X		X							X	X					10	0.439	-83.949	188.956	7.299	0.010
40		X						X	X			X		X								X		X				X	10	0.819	-89.667	200.392	18.735	0.000
7		X		X				X	X		X	X		X									X					X	9	0.159	-90.98	200.821	19.165	0.000
33		X						X	X		X	X	X										X	X			X	X	11		-88.995	201.265	19.609	0.000
8		X		X	X			X	X		X	X				X													11		-89.05	201.375	19.719	0.000
12		X		X	X			X	X		X	X																	9		-91.359	201.579	19.923	0.000
26		X		X	X			X	X		X	X		X		X						X	X	X					11		-89.444	202.163	20.507	0.000
5		X	X		X			X	X		X	X	X	X		X							X						13		-87.638	203.052	21.395	0.000
13		X		X	X	X		X	X		X	X		X									X						10		-91.054	203.166	21.509	0.000
6		X		X	X			X	X		X	X	X			X							X						12		-88.999	203.513	21.856	0.000
15		X		X	X			X	X		X	X		X									X						7		-94.519	203.569	21.912	0.000
4	X	X		X	X			X	X		X	X	X	X		X																		

Table 2.6. Variables that best predict *H. scutatum* nests at shoreline points of 35 Maine wetlands with nests, 2002-2003.

Variable	Importance ranking of variable <sup>a</sup>	Logistic regression parameters from best model		Descriptive data for important variables					
				Nest points			Unoccupied points		
		$\beta$	SE	$\bar{x}$	SD	Range or sum	$\bar{x}$	SD	Range or sum
Slope	1	+0.05	0.01	75.41	15.71	30-90	52.92	27.21	8-90
Maximum depth (cm) within 2m	1	+0.05	0.02	35.02	29.85	10-250	19.69	13.21	4-68
Nest vegetation depth (cm)	1	+0.09	0.04	11.22	5.33	3-27	7.69	5.04	0-29
<i>Ilex verticillata</i>	1	+1.29	0.70	13%	33%	11	7%	25%	9
Any moss	1	+16.62	425.79	100%	0%	88	88%	33%	115
Water depth under nest (cm)	0.99	+0.09	0.04	15.35	11.70	0-76	7.23	5.87	0-28
FO4 (10m) <sup>b</sup>	0.961	-1.51	0.57	13%	33%	11	25%	43%	32
<i>Spiraea alba</i>	0.961	-1.34	0.71	11%	32%	10	12%	33%	16
<i>Chamaedaphne calyculata</i>	0.934	-2.30	0.89	5%	21%	4	8%	28%	11
<i>Kalmia angustifolia</i>	0.816	-9.77	43.32	1%	11%	1	2%	15%	3

<sup>a</sup> Sum of Akaike Weights for models containing the variable (Burnham and Anderson 2002); see table 2.5 for weights.

<sup>b</sup> FO4 = coniferous forest NWI class, EM = emergent NWI class (Cowardin et al. 1979).

<sup>c</sup> Variable not in most parsimonious model, thus, no logistic regression parameter applicable.

Table 2.7. Confusion matrix showing classification rate (0.5 threshold) of independent data in the model that best predicts *H. scutatum* nest occupancy at shoreline points in 35 Maine wetlands.

		Observed data	
		Occupied	Unoccupied
Predicted by model	Occupied	37	11
	Unoccupied	9	61

wetlands with nests, 131 from wetlands without nests), and evaluation ( $n = 147$ ; 72 from wetlands with nests, 75 from wetlands without nests). During exploratory analysis, I omitted the same variables as in the model of nest site location along shoreline of occupied wetlands (Table 2.2). I calculated and ranked 39 logistic regression models with AIC<sub>c</sub> (Table 2.8). The most parsimonious models are indicated by large Akaike Weights in Table 2.8. I ranked variables by importance, and variables with summed Akaike Weight of  $> 0.3$  are presented with their descriptive data in Table 2.9. The positive or negative association of a variable is indicated by ( $\beta$ ) (Table 2.9).

Unoccupied, shoreline points in wetlands with *H. scutatum* nests contained dead wood substrate, water flow, *Sphagnum* spp. for egg attachment, presence of blue-joint reed grass (*Calamagrostis canadensis*), *Spiraea tomentosa*, sensitive fern (*Onoclea sensibilis*), and *Spiraea alba* within 1m (Tables 2.8 and 2.9). These shoreline points did not contain *Kalmia angustifolia* within 1m or deciduous forest NWI class within 10 m (Tables 2.8 and 2.9). The best logistic regression model describing shoreline points in occupied as opposed to unoccupied wetlands (Table 2.9) was used to classify an independent data set (Table 2.10). The model correctly classified 99 (67%) of 147 points (Table 2.10).

I present the mean, *SD*, and range of variables collected at shoreline points with nests, unoccupied shoreline points in wetlands with nests, and unoccupied shoreline points in unoccupied wetlands based on all data collected (i.e., exploratory, model building and evaluation) (Table 2.11). The patterns shown by the models (Tables 2.5 and 2.8) are visible also in these data, presented for descriptive purposes. A continuum in mean value is evident for many variables. For example, at nest points, mean slope is 76



Table 2.9. Variables best predicting *H. scutatum* nesting in wetlands, based on available shoreline points sampled in 67 Maine wetlands, 2002-2003.

Variable	Importance ranking of variable <sup>a</sup>	Logistic regression parameters from best model		Descriptive data for unoccupied points					
		<i>B</i>	<i>SE</i>	Wetlands with nests			Wetlands without nests		
				$\bar{x}$	<i>SD</i>	Sum	$\bar{x}$	<i>SD</i>	Sum
<i>Calamagrostis canadensis</i>	1	+1.458	0.549	17%	37%	24	4%	20%	5
<i>Spiraea tomentosa</i>	1	+2.938	1.063	15%	35%	21	1%	9%	1
flow	0.999	+0.820	0.443	15%	36%	22	8%	27%	10
<i>Kalmia angustifolia</i>	0.999	-1.699	0.680	2%	14%	3	12%	33%	16
<i>Onoclea sensibilis</i>	0.999	+1.537	0.707	9%	29%	13	2%	15%	3
FO1 (10m) <sup>b</sup>	0.997	-0.668	0.295	28%	49%	37	40%	49%	52
wood substrate	0.996	+1.294	0.362	31%	47%	45	12%	32%	15
<i>Spiraea alba</i>	0.995	+0.737	0.446	13%	34%	19	8%	28%	11
eggs attached to <i>Sphagnum</i>	0.348	+0.485	0.301	69%	47%	99	63%	48%	83

<sup>a</sup> Sum of Akaike Weights for models containing the variable (Burnham and Anderson 2002); weights are provided in table 2.7.

<sup>b</sup> FO1 = Deciduous forest NWI class, SS = shrub scrub NWI class (Cowardin et al. 1979).

<sup>c</sup> Variable not in most parsimonious model, thus, no logistic regression parameter applicable.

Table 2.10. Confusion matrix showing classification rate (0.5 threshold) of independent data in the model that best predicts wetlands with *H. scutatum* nests, based on habitat data collected at shoreline points without nests in 67 Maine, 2002-2003.

		Observed data	
		Occupied	Unoccupied
Predicted by model	Occupied	49	25
	Unoccupied	23	50

Table 2.11. Data range of variables important in distinguishing shoreline points with nests ( $n = 239$ ), random points ( $n = 294$ ) in wetlands with nests, and random points ( $n = 258$ ) in wetlands without nests based on all data collected in 67 Maine wetlands, 2002-2003.

Variable	Nest points				Unoccupied points in nesting wetlands				Unoccupied points in unoccupied wetlands		
	$\bar{x}$	$SD$	Range or sum	Model 1 <sup>b</sup>	$\bar{x}$	$SD$	Range or sum	Model 2 <sup>c</sup>	$\bar{x}$	$SD$	Range or sum
Nest vegetation (cm)	11.36	5.15	3-27	x	7.33	4.85	0-29		6.42	4.87	0-32
Slope	76.45	14.85	30-90	x	51.70	27.21	5-90		47.88	27.31	1-90
Max. depth (cm)	31.91	23.71	0-250	x	24.32	25.14	2-250		25.92	23.90	4-120
Water depth (cm)	14.16	10.96	0-76	x	7.48	6.39	0-40		7.66	12.60	0-110
<i>Ilex verticillata</i>	58 %	36 %	31	x	7 %	25 %	19		9 %	29 %	24
Moss spp.	98 %	14 %	194		84 %	37 %	246		84 %	37 %	216
Conifer 10 m	6 %	23 %	11	x	11 %	31 %	32		11 %	32 %	1-29
<i>Chamaedaphne calyculata</i>	6 %	24 %	12	x	8 %	27 %	23		14 %	35 %	36
<i>Kalmia angustifolia</i>	2 %	12 %	3	x	2 %	14 %	6	x	12 %	32 %	30
<i>Spiraea alba</i>	12 %	33 %	24	x	11 %	31 %	31	x	8 %	27 %	20
Deciduous 10 m	17 %	38 %	34		13 %	33 %	37	x	20 %	40 %	52
<i>sphagnum</i> spp egg attachment	82 %	38 %	161		67 %	47 %	196	x	68 %	47 %	175
wood substrate	46 %	50 %	90		28 %	45 %	82	x	12 %	32 %	30
flow	26 %	44 %	51		20 %	40 %	58	x	11 %	31 %	27
<i>Calamagrostis canadensis</i>	29 %	46 %	58		22 %	42 %	66	x	5 %	23 %	14
<i>Onoclea sensibilis</i>	7 %	26 %	14		10 %	29 %	28	x	3 %	16 %	1
<i>Spiraea tomentosa</i>	17 %	38 %	34		15 %	35 %	43	x	0.4 %	6 %	1

<sup>a</sup> All data from exploratory, model building and evaluation sets.

<sup>b</sup> Variables in best model predicting nests from unoccupied points in wetlands with nests (83% correct classification rate).

<sup>c</sup> Variables in best model predicting occupied wetlands through comparing unused points in occupied and unoccupied wetlands (67% correct classification rate).

degrees, whereas, at random, unoccupied shoreline points in wetlands with nests the slope is 52 degrees; and at random, unoccupied shoreline point in unoccupied wetlands the slope is 48 degrees (Table 2.11). The *SD* and range of shoreline slope is small at nest locations and is large in unoccupied shoreline points in wetlands with and without nests (Table 2.11). *H. scutatum* nests are disproportionately located in shoreline points with certain characteristics (e.g., steep slope, deep nest vegetation, wood substrate, water flow, presence of *Ilex verticillata* and moss within 1 m and absence of *Kalmia angustifolia* in 1 m and conifer NWI class in 10 m) as compared with available habitat at all wetlands (Table 2.11).

### **Co-occurring Wetland Species**

Unidentified fish species were present in at least 6 (17.1%) of 35 wetlands with nesting *H. scutatum* and 7 (21.9%) of 32 wetlands without nesting *H. scutatum*. Co-occurring amphibian species were anecdotally detected in wetlands with ( $n = 35$ ) and in wetlands without ( $n = 32$ ) *H. scutatum* nests (Table 2.12). *A. maculatum* is the only species for which the detection of both presence and absence is rigorous; the outer layer of jelly from this species' egg masses was visible throughout the survey period. In 11 wetlands *H. scutatum* occurred without *A. maculatum*.

## **DISCUSSION**

Understanding species-habitat relationships is requisite for inventorying, monitoring, and researching amphibian populations and designing conservation and mitigation plans. I present models of wetland and shoreline habitat used by nesting *H. scutatum* that are based on empirical data and evaluated with independent data sets or

Table 2.12. Amphibian species anecdotally detected in 35 wetlands with *H. scutatum* and 32 wetlands without *H. scutatum* in Maine, 2002-2003.

Species	Number of wetlands in which species detected	
	<i>H. scutatum</i> present	<i>H. scutatum</i> absent
Spotted salamander ( <i>Ambystoma maculatum</i> )	24	16
Green frog ( <i>Rana clamitans</i> )	18	17
Spring peeper ( <i>Pseudacris crucifer</i> )	18	7
Wood frog ( <i>Rana sylvatica</i> )	17	9
Red backed salamander ( <i>Plethodon cinereus</i> )	15	11
Pickerel frog ( <i>Rana palustris</i> )	13	5
Bull frog ( <i>Rana catesbiana</i> )	9	9
Red spotted newt ( <i>Notophthalmus viridescens</i> )	5	4
Two-lined salamander ( <i>Eurycea bislineata</i> )	2	2
Grey treefrog ( <i>Hyla versicolor</i> )	2	0
American toad ( <i>Bufo americanus</i> )	0	2

jackknifing. The descriptions of the wetlands and the shoreline structure used by *H. scutatum* should be relevant throughout this species' range. Plant species associated with *H. scutatum* nests will be most relevant in regions with similar plant communities, including New England, the Canadian Maritimes, and the upper Midwest.

### **Characteristics of Wetlands With Nests**

Describing the 'typical' wetlands used by *H. scutatum* is a challenge due to the diversity of wetlands occupied by this species and the diverse ways of characterizing wetlands (e.g., hydrological, chemical, geological, morphological, vegetative, faunal). I observed that *H. scutatum* were typically found nesting in either marshes with a history of beaver activity or wetlands with a forested canopy and some input from groundwater (e.g., seeps or slow-moving, seasonal streams) (Figure 2.2). These attributes are not easily detected with GIS or aerial photos, but can be readily detected in the field throughout the year. These types of wetlands may have functional similarities including a hydroperiod that persists into July or August, stable water levels that do not flood during nesting (perhaps due to flood control provided by beaver dams or the regular inflow of seeps), and steep shoreline (e.g., beaver-made stumps and logs, base of *I. verticillata* and *A. rubrum* in seeps). Other wetlands with nesting *H. scutatum* included large, beaver-dammed ponds with fish; natural and human-constructed, isolated vernal pools; and fens. I did not find *H. scutatum* in 3 bogs searched in ANP. Other wetlands in which the species was not typically found include wetlands that dried in June or July, before metamorphosis, and had low pH (e.g., vernal pools, fens, and coniferous, forested wetlands) and inlets to large bodies of water that flooded during the nesting period.

Variables in the wetland scale model that best predicted occupation of wetlands by nesting *H. scutatum* include pH (+) and shrub scrub (-) and unconsolidated bottom (-) NWI classes. Shrub scrub and unconsolidated bottom NWI wetland classes were negative predictors of *H. scutatum* presence. These types of wetlands seemed to dry in June or July, before metamorphosis, and lacked steep, mossy shoreline. Stream connectivity of a wetland and flow (i.e., at the shoreline point scale) are positive predictors of *H. scutatum* presence. These conditions may provide nutrient inflow, extend hydroperiod, or provide favorable habitat along which juveniles disperse. Forest adjacent to wetlands was typically mixed forest (54 of 67 wetlands) and was not a useful predictor of nest occurrence.

Wetlands occupied by *H. scutatum* in this study had higher pH than wetlands without the species. A possible benefit of higher pH for *H. scutatum* larvae may be greater prey abundance because of greater productivity typically associated with wetlands with higher pH (Mitsch and Gosselink 2000). A negative affect of low pH on larvae is lowered sodium uptake and increased sodium loss, which can lead to death (Pierce 1985, Ferraro and Burgin 1993). Nests maintain moisture from rain or by wicking water from pools, and if the water has low pH, development of embryos may be delayed or inhibited (Pierce 1985). Considerable interspecific variation in the tolerance of amphibians to acidity occurs (Pierce 1985). I am unaware of data that depict *H. scutatum* as more tolerant to acidity than other species. It is probable that *H. scutatum* are vulnerable to human-induced acidification of wetlands, which has lowered the pH of wetlands throughout the species' range, including Maine (e.g., Heath 1993).

Petranka (1998), NatureServe (2004), and Johnson (1985) suggest that *H. scutatum* are a bog species. My data indicate that *H. scutatum* 1) occur in wetlands with a higher average pH (i.e., 5.5) than unoccupied wetlands, 2) is not present in 3 bogs I searched (i.e., bog ponds in Great Heath, bog south of Hio Road, bog pond in south inlet to Jordan Pond, ANP), and 3) is negatively associated with *K. angustifolia* and *C. calyculata*, plant species typically found in fens in my study area (Calhoun 1994). It is possible that wetlands used by this species in Maine differ from wetlands used in other parts of this species' range. It is also possible that the term "bog" is applied to different types of wetlands (e.g., marshes, fens) in other studies. I frequently found *H. scutatum* in marshes, occasionally found *H. scutatum* in richer fens, and did not find *H. scutatum* in bogs, based on the chemo-hydrological definition of Maine bogs provided by Davis and Anderson (2001). Maine peatlands are either fens, which are minerotrophic, or bogs, which are ombrotrophic (i.e., minerals received by the plants come entirely from the atmosphere) (Davis and Anderson 2001). Maine bogs are raised by peat accumulation above the surrounding water table, and are thus distinguished from acidic or poor fens with the same dominant vascular plant species as found in bogs and *Sphagnum* dominating in the ground cover (Davis and Anderson 2001).

Predictor variables of wetland occupancy, based on shoreline point metrics, include availability of *Sphagnum* spp. along the shoreline (+), dead wood substrate (+), water flow (+), the presence of plant species *C. canadensis* (+), *S. tomentosa* (+), *O. sensibilis* (+), and *S. alba* (+) within 1 m, the absence of *K. angustifolia* (-) within 1 m, and the absence of deciduous forest NWI class in 10m (-). Plant species (e.g., *S. alba*, *S. tomentosa*, *O. sensibilis*, and *C. canadensis*) positively associated with *H. scutatum*

typically grow in wet meadows or deciduous forested wetlands with well-developed shrub and herbaceous layers, wetlands that typically have higher nutrients and a consistently moist hydrological setting (Calhoun 1994). Plant species negatively associated with *H. scutatum* (e.g., *K. angustifolia*, *C. calyculata*) typically grow in wetlands with lower pH (Calhoun 1994). The presence of sphagnum and dead wood substrate forming the shoreline are indicative of a wetland suitable for *H. scutatum* nesting. Sphagnum seemed provide appropriate nest conditions and to be correlated with appropriate hydrology. Dead wood provided a steep substrate on which moss frequently colonized. More information on substrate characteristics at nests is available in Chapter 1. Dead wood substrate seemed more abundant in wetlands with past beaver occupation (and thus correlated with water flow, higher nutrients, longer hydroperiod, and fish).

*H. scutatum* larvae are palatable to fish (Kats et al. 1988) and Petranka (1998) suggests that fish presence is negatively correlated with *H. scutatum* nest presence. I found that fish (unknown spp.) occupied at least 6 (17.1%) of 35 wetlands inhabited by nesting *H. scutatum*. Carnivorous fish may compete with or prey on *H. scutatum*. Herbivorous fish will not have a predatory or competitive effect on *H. scutatum* larvae, which, like all salamanders, are carnivorous. Larvae may be able to avoid fish by inhabiting pools isolated from other parts of a wetland (*personal observation*), shallows not navigable by most fish (*personal observation*), or refugia such as organic muck or submerged sphagnum. Alternately, larvae may occur in wetlands with fish, but successfully metamorphose only during years when fish are absent. All wetlands with fish, in this study, also contained signs of beaver activity, which suggests that some years these wetlands may be fishless.

Vernal pools are bodies of water 1) defined by their breeding animal community (e.g., *Ambystoma* spp., *R. sylvatica*, fairy shrimp (*Anostraca* spp.)) (e.g., Tappan 1997, Maine Audubon Society 1999, Kenney and Burne 2001), 2) that are or become isolated while containing water (Kenney and Burne 2001), 3) that have wet-dry cycles that preclude permanent populations of fish (Kenney and Burne 2001), and 4) are seasonal or, if permanent, tend to be shallow enough to exclude adult fish populations by becoming anoxic in the summer or freezing in winter (Maine Audubon Society 1999). *H. scutatum* have not typically been included as a species that defines a vernal pool, although they can breed in vernal pools (e.g., Tappan 1997, Maine Audubon Society 1999, Kenney and Burne 2001). My data confirm the facultative status of *H. scutatum* use of vernal pools. I found *H. scutatum* in 21 wetlands I defined as vernal pools using a broad definition of the term (e.g., including large marshes and forested seeps that partially dried), and 23 vernal pools did not have *H. scutatum*. In wetlands that were not vernal pools, *H. scutatum* were present in 10 and absent in 5.

### **Characteristics of Shoreline Points With Nests**

In wetlands with nesting *H. scutatum*, shoreline points with nests were characterized by variables of steep shore slope, deep water by shoreline and nearby, deep shoreline vegetation, presence of moss, and absence of conifer NWI class, *S. alba*, *C. calyculata*, and *K. angustifolia*. Nests were positioned on steep shore above deep water, presumably so that the aquatic larvae are able to drop into water upon hatching, even after water levels recede during the 5 - 8 weeks of embryo development (Chapter 1, Harris in press, Richmond 1999). The availability of steep locations with appropriate shoreline vegetation over deep water may constrain where females will lay eggs. Steep

shoreline seems to be provided by wood (e.g., logs, stumps and roots frequently found in beaver- or human-flooded wetlands), red maple (*Acer rubrum*) trees, *I. verticillata* stems, tussock sedge (*Carex stricta*), and occasionally steep earth banks (usually in human-created wetlands) and rocks. Moss appears to provide consistent moisture and a structure loose enough for the salamander to enter, yet dense enough to provide concealment. Nests that were laid in deep shoreline vegetation seemed to be moist even during hot, dry weather. Some nests were in litter from grasses, sedges, and ferns (Chapter 1).

The vegetation negatively associated with nest points (i.e., coniferous class, *S. alba*, *C. calyculata*, and *K. angustifolia*) is typical of low pH (Calhoun 1994). *S. alba* had a positive association with nesting wetlands, but within wetlands with nests, the association was negative. However, the total data (Table 2.11) showed a positive relationship, including in wetlands with *H. scutatum* nests. My perception is that *S. alba* is positively associated with hydrological and nutrient conditions appropriate for *H. scutatum*, but does not reliably provide structure on which moss could grow, thus, the species is a relatively neutral indicator of nest presence at the shoreline scale.

I measured variables (e.g., temperature, canopy cover) once at each shoreline point, which did not take into account variation due to date, time, and weather. The influence of temperature and canopy cover on *H. scutatum* was probably confounded by variation related to measurement date and time. For example, at the beginning of nesting season in April, canopy cover over nests was 0%, but increased throughout the study period. The negative association of coniferous forest within 5 m<sup>2</sup> of occupied shoreline points may be due to shorter hydroperiod or lack of shoreline moss potentially associated with this vegetation class.

## Management Recommendations

I found *H. scutatum* in low densities (Chapter 1), suggesting that continued concern for this species is warranted in Maine. Habitat management for *H. scutatum* may be accomplished by protecting individual wetlands and wetland complexes along with surrounding upland habitat. Wetland-breeding amphibian species require specific types of wetland and upland habitat for juvenile and adult life stages (e.g., Guerry 2000), and they require nearby wetlands from which to re-colonize extirpated populations (e.g., Sjögren-Gulve 1994, Corser and Dodd 2004). Research on the wetland and surrounding upland habitat that supports populations over the long term is especially needed. The habitat requirements of the terrestrial stages of the *H. scutatum* lifecycle (i.e., adult, juvenile) are virtually unknown. Research on the attributes of upland habitat required by *H. scutatum* and the dispersal and migratory distance traveled by this species from wetlands is needed.

The current habitat of a species may not be the optimal habitat (Gray and Craig 1991) or may represent recovery of previously modified habitat. The habitat models presented here, thus, may not represent the optimal habitat of the species because 1) nests may be present where conditions are inappropriate for embryo or larval success and 2) apparently unoccupied wetlands may have nests during other years because females do not breed every year (Harris and Ludwig 2004) and nesting populations fluctuate (Corser and Dodd 2004). However, *H. scutatum* use specialized nesting habitat, exhibit wetland philopatry (Harris and Ludwig 2004), and seem to exhibit nest point fidelity (*personal observation*), which may reduce the number of and the variation in wetlands and shoreline habitat in which nesting occurs. Specialized search efforts are needed to survey

*H. scutatum*. I recommend conducting surveys for nests during May and June (Chapter 1) at wetlands with the following characteristics developed from predictive models: high pH (5.5); steep shoreline (60 - 90°); deep (11 cm) shoreline moss or other nesting vegetation; deep (15 cm) near shore water; deep (35 cm) basin depth; and the presence of moss, *C. canadensis*, *S. tomentosa*, and *I. verticillata*. The definitions of wetland and shoreline habitat presented here will improve the ability of land managers and researchers to evaluate potentially suitable habitat for *H. scutatum*. An improved ability to identify suitable habitat will provide guidance for surveys of the species and for identifying types of habitat to be managed or conserved.

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## APPENDIX A. Conservation ranking of *H. scutatum* in North America.

Table A.1. State, province, and NatureServe rankings of *H. scutatum*.

State/ Province	Nature-Serve Rank	State/ Province Rank	Citation for State/Province Rank
Maine	S3	SC	<a href="http://www.state.me.us/ifw/wildlife/03report/etss.htm">www.state.me.us/ifw/wildlife/03report/etss.htm</a>
New Hampshire	S3S4		<a href="http://www.wildlife.state.nh.us/Wildlife/Nongame/species_list.htm">www.wildlife.state.nh.us/Wildlife/Nongame/species_list.htm</a>
Vermont	S2	SC	<a href="http://www.vtfishandwildlife.com/wildlife_nongame.cfm">www.vtfishandwildlife.com/wildlife_nongame.cfm</a>
Massachusetts	S3	SC	<a href="http://www.mass.gov/dfwele/dfw/nhosp/nhrare.htm">www.mass.gov/dfwele/dfw/nhosp/nhrare.htm</a>
Connecticut	S4		<a href="http://dep.state.ct.us/cgnhs/nddb/amphib.htm">http://dep.state.ct.us/cgnhs/nddb/amphib.htm</a>
Rhode Island	S3		<a href="http://www.state.ri.us/dem/programs/bpoladm/plandev/heritage/pdf/animals.pdf">www.state.ri.us/dem/programs/bpoladm/plandev/heritage/pdf/animals.pdf</a>
New York	S5		<a href="http://www.dec.state.ny.us/website/dfwmr/heritage/animallist.pdf">www.dec.state.ny.us/website/dfwmr/heritage/animallist.pdf</a>
Pennsylvania	S4		<a href="http://www.pacode.com/secure/data/058/chapter75/chap75toc.html">www.pacode.com/secure/data/058/chapter75/chap75toc.html</a>
New Jersey	S3		<a href="http://www.state.nj.us/dep/fgw/ensp/pdf/spclspp.pdf">www.state.nj.us/dep/fgw/ensp/pdf/spclspp.pdf</a>
Delaware	S1	SC	<a href="http://www.dnrec.state.de.us/fw/animal.htm#amphibians">www.dnrec.state.de.us/fw/animal.htm#amphibians</a>
D.C.	SH		
Maryland	S5		<a href="http://dnrweb.dnr.state.md.us/download/rteanimals.pdf">http://dnrweb.dnr.state.md.us/download/rteanimals.pdf</a>
Virginia	S5		<a href="http://vafwis.org/WIS/visitor/species.asp?ln=V&amp;sID=33943&amp;nav=species">http://vafwis.org/WIS/visitor/species.asp?ln=V&amp;sID=33943&amp;nav=species</a>
West Virginia	S5		<a href="http://www.wvdnr.gov/Wildlife/PDFFiles/ANIMALSNEW.pdf">www.wvdnr.gov/Wildlife/PDFFiles/ANIMALSNEW.pdf</a>
North Carolina	S3	SC	<a href="http://216.27.49.98/pg07_WildlifeSpeciesCon/protected_species.pdf">http://216.27.49.98/pg07_WildlifeSpeciesCon/protected_species.pdf</a>
South Carolina	SNR		<a href="http://www.dnr.state.sc.us/pls/heritage/county_species.list?pcounty=all">www.dnr.state.sc.us/pls/heritage/county_species.list?pcounty=all</a>
Mississippi	S1S2	-	<a href="http://www.mdwfp.com/museum/downloads/tandelist.pdf">www.mdwfp.com/museum/downloads/tandelist.pdf</a>
Alabama	S3	no list	<a href="http://www.outdooralabama.com/watchable-wildlife/regulations/endangered-species.cfm">www.outdooralabama.com/watchable-wildlife/regulations/endangered-species.cfm</a>
Georgia	S3	S3	<a href="http://georgiawildlife.dnr.state.ga.us/content/specialconcernanimals.asp">http://georgiawildlife.dnr.state.ga.us/content/specialconcernanimals.asp</a>
Florida	S2	-	<a href="http://www.floridaconservation.org/pubs/endanger.html#amph">www.floridaconservation.org/pubs/endanger.html#amph</a>
Oklahoma	S1	SC	<a href="http://www.wildlifedepartment.com/endanger2.htm">www.wildlifedepartment.com/endanger2.htm</a>
Arkansas	S2	S2	<a href="http://www.naturalheritage.com/publications/rare/pdfs/Inventory_List-Animals.pdf">www.naturalheritage.com/publications/rare/pdfs/Inventory_List-Animals.pdf</a>
Tennessee	S3	need management	<a href="http://www.state.tn.us/twra/nong002.html">http://www.state.tn.us/twra/nong002.html</a>
Kentucky	S4	no list	<a href="http://www.natureserve.org/explorer/servlet/NatureServe?searchName=HEMIDACTYLUM+SCUTATUM+">www.natureserve.org/explorer/servlet/NatureServe?searchName=HEMIDACTYLUM+SCUTATUM+</a>
Missouri	S4		<a href="http://www.conservation.state.mo.us/documents/nathis/endangered/animals_concern.pdf">www.conservation.state.mo.us/documents/nathis/endangered/animals_concern.pdf</a>
Minnesota	S3		<a href="http://midwest.fws.gov/endangered/lists/minnesota04-spp.pdf">http://midwest.fws.gov/endangered/lists/minnesota04-spp.pdf</a>
Michigan	S5		<a href="http://web4.msue.msu.edu/mnfi/data/animal_list.pdf">http://web4.msue.msu.edu/mnfi/data/animal_list.pdf</a>
Wisconsin	S3	SC-H	<a href="http://www.dnr.state.wi.us/org/land/er/working_list/taxalists/herps.htm">www.dnr.state.wi.us/org/land/er/working_list/taxalists/herps.htm</a>
Illinois	S2	T	<a href="http://www.inhs.uiuc.edu/cbd/ilspecies/amphsplist.html">www.inhs.uiuc.edu/cbd/ilspecies/amphsplist.html</a>
Indiana	S2	E	<a href="http://herpcenter.ipfw.edu/index.htm?http://herpcenter.ipfw.edu/outreach/INspecies.htm&amp;2">http://herpcenter.ipfw.edu/index.htm?http://herpcenter.ipfw.edu/outreach/INspecies.htm&amp;2</a>
Ohio	S3	no list	<a href="http://www.dnr.state.oh.us/endangered/endangered4.htm">www.dnr.state.oh.us/endangered/endangered4.htm</a>
New Brunswick	S1	S1	<a href="http://www.accdc.com/products/profiles/salamander.html">www.accdc.com/products/profiles/salamander.html</a>
Nova Scotia	S3	sensitive	<a href="http://www.gov.ns.ca/natr/wildlife/genstatus/ranks.asp">www.gov.ns.ca/natr/wildlife/genstatus/ranks.asp</a>
Quebec	S2		
Ontario	S4	S4	<a href="http://www.mnr.gov.on.ca/MNR/nhic/species/listout.cfm?el=aa">www.mnr.gov.on.ca/MNR/nhic/species/listout.cfm?el=aa</a>
All of Canada		NAR	<a href="http://www.cosewic.gc.ca/pdf/English/Prioritized_List_e.pdf">www.cosewic.gc.ca/pdf/English/Prioritized_List_e.pdf</a>

**APPENDIX B. Maps of 67 wetland sites surveyed for *H. scutatum* in Maine, 2002-2003.**

Figure B.1. Sites surveyed in Acadia National Park, Seawall region.

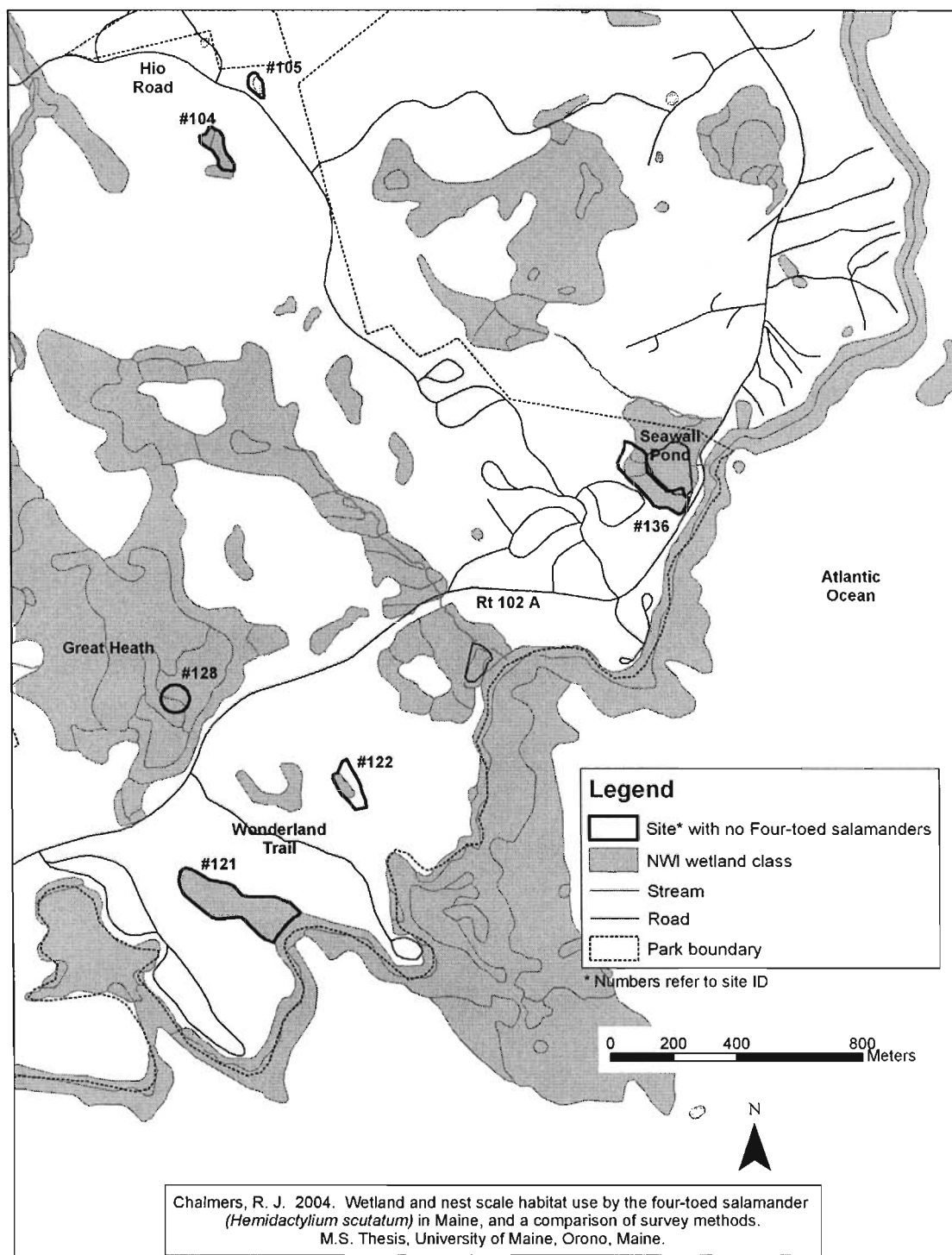


Figure B.2. Sites surveyed in Acadia National Park, Seal Cove Road region.

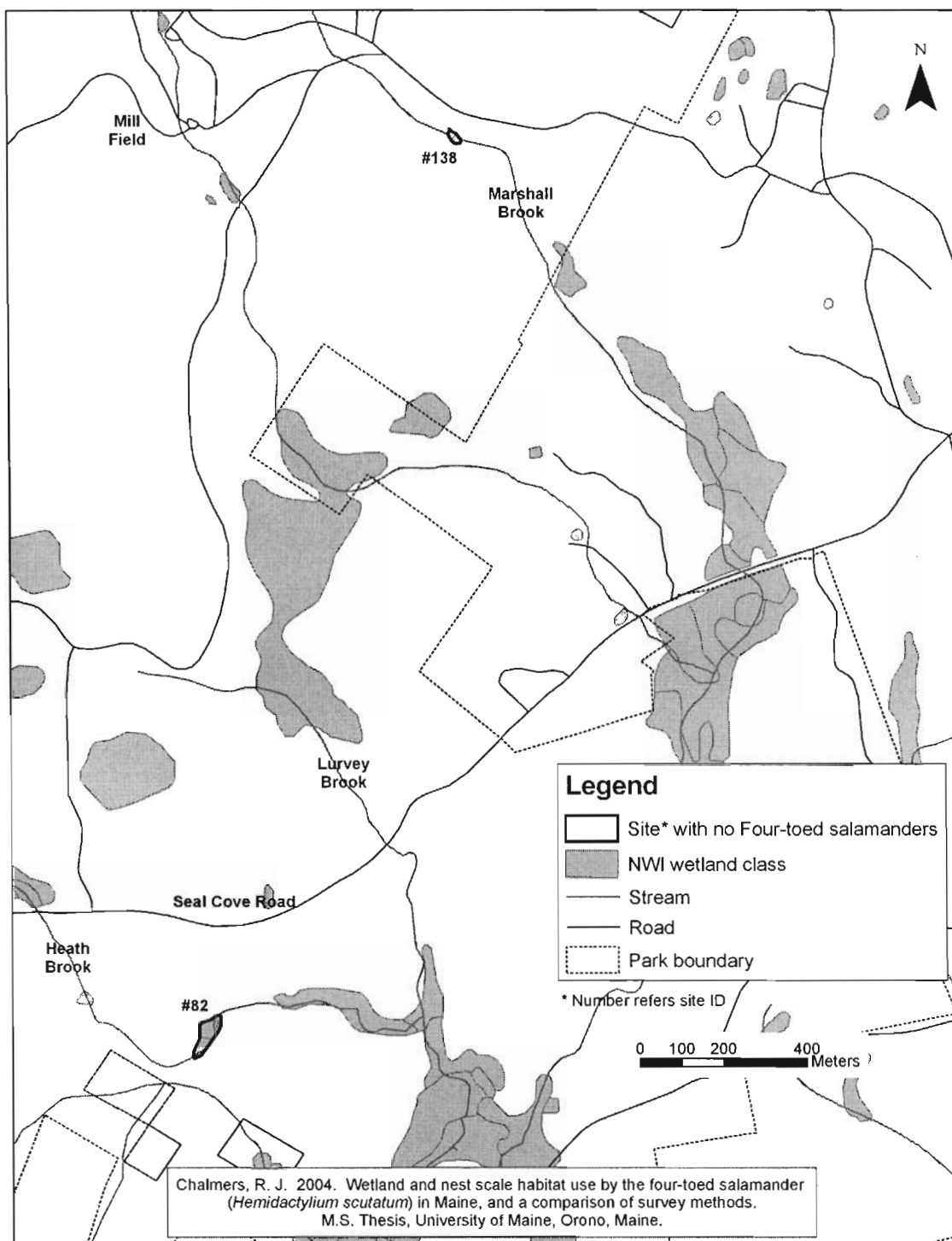


Figure B.3. Sites surveyed in Acadia National Park, Seal Cove Pond region.

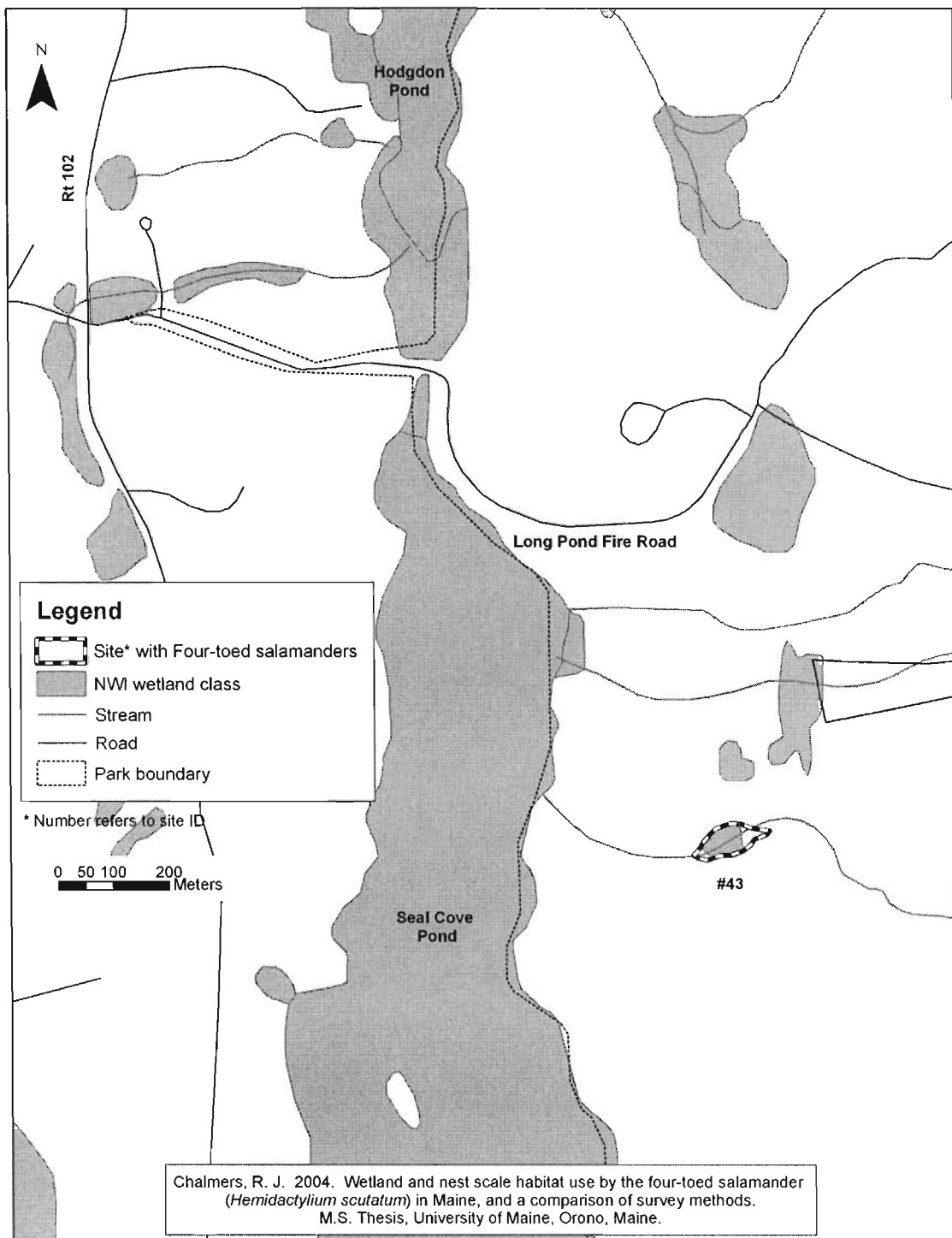


Figure B.4. Sites surveyed in Acadia National Park, Long Pond Fire Road region.

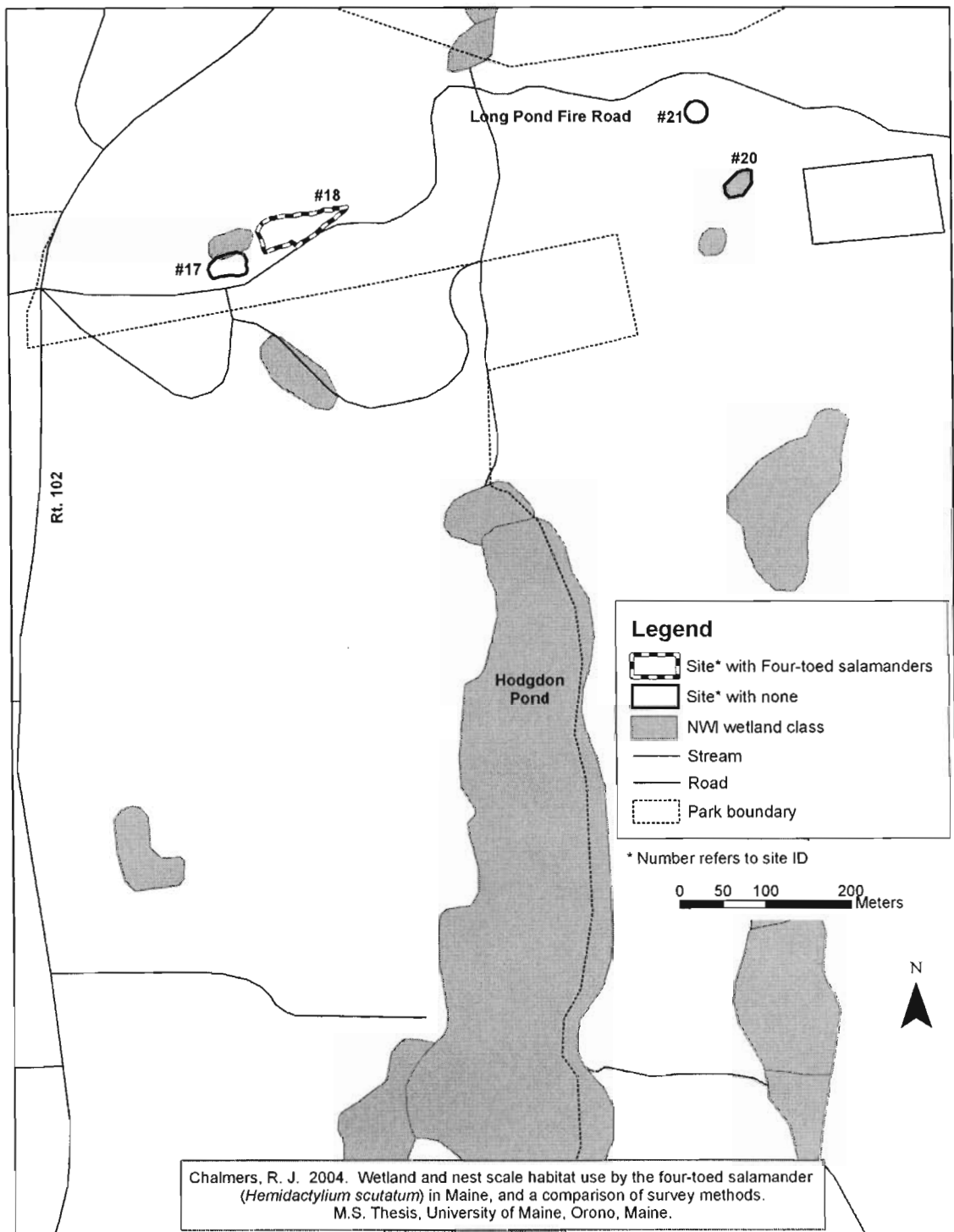


Figure B.5. Sites surveyed in Acadia National Park, Witch Hole Pond region.

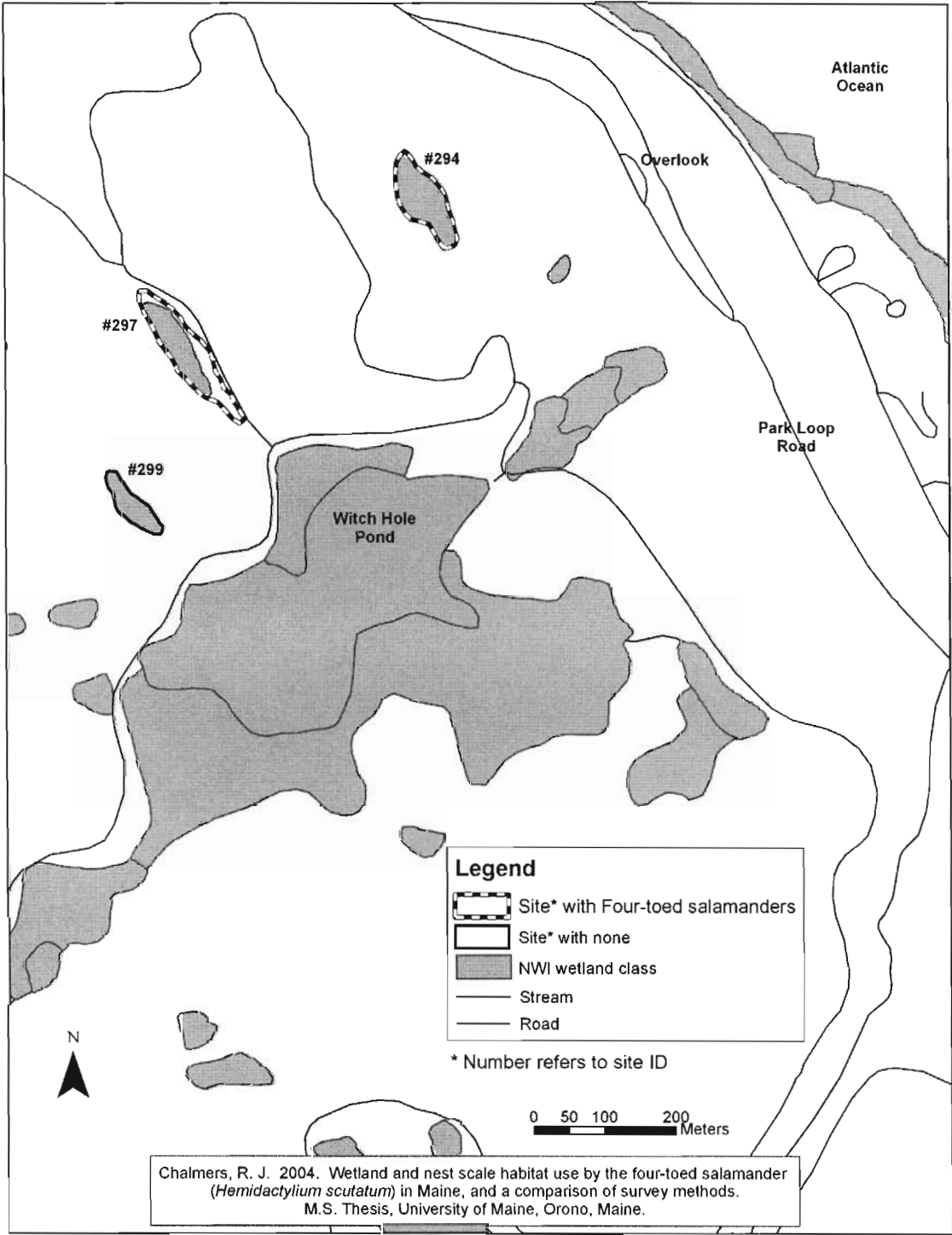


Figure B.6. Sites surveyed in Acadia National Park, Bar Harbor region.

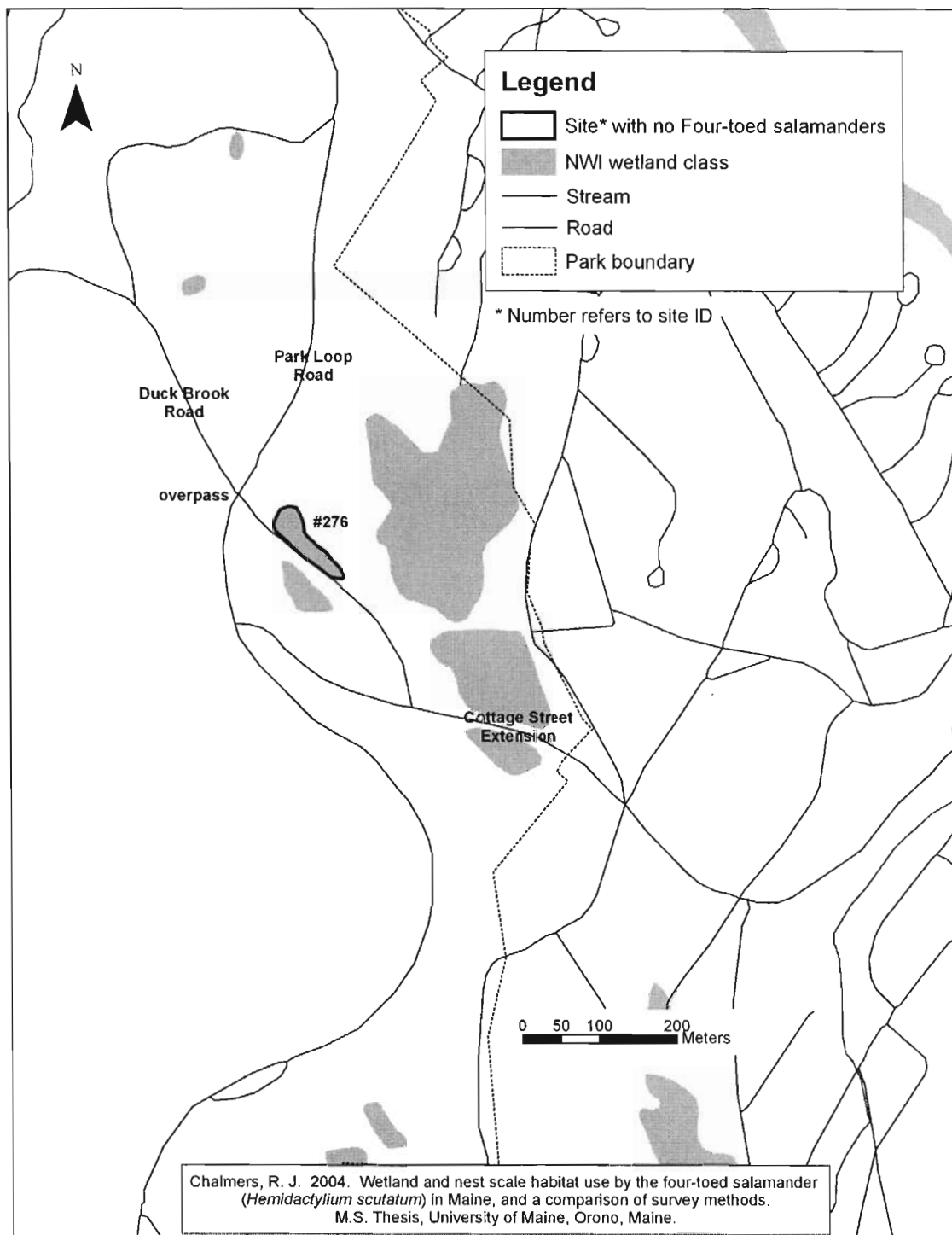


Figure B.7. Sites surveyed in Acadia National Park, Duck Brook Road region.

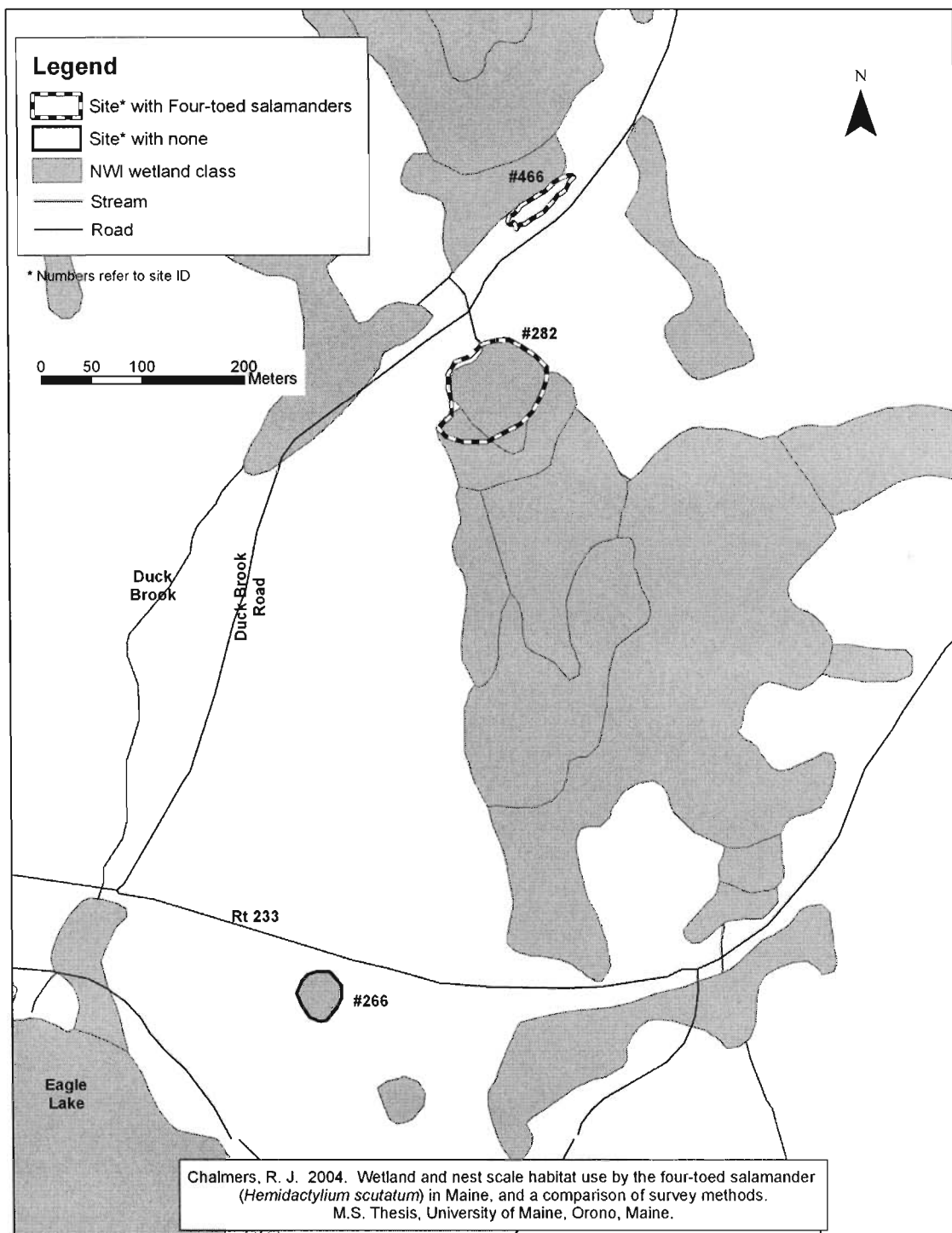


Figure B.8. Sites surveyed in Acadia National Park, Lake Wood region.

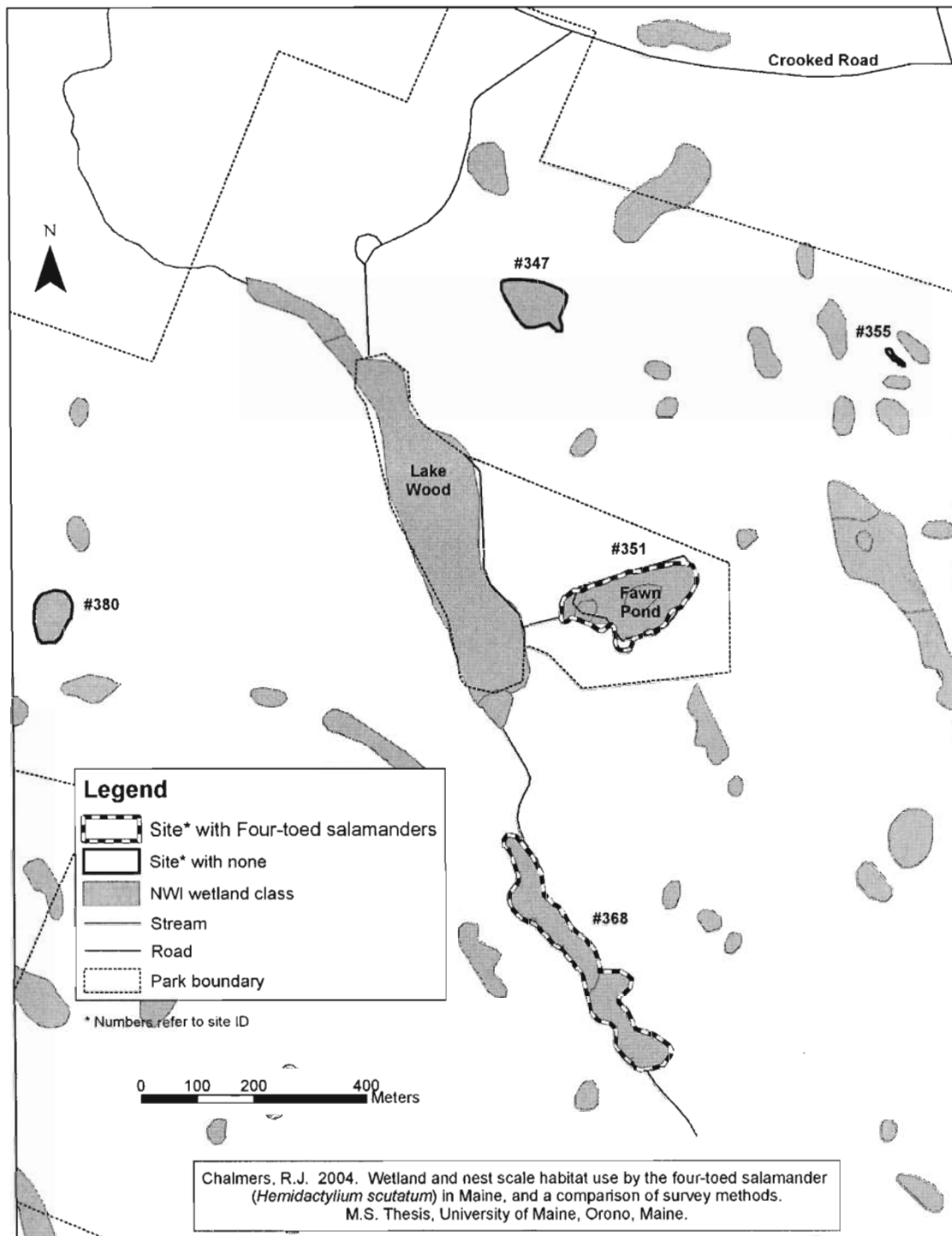


Figure B.9. Sites surveyed in Acadia National Park, Breakneck Stream region.

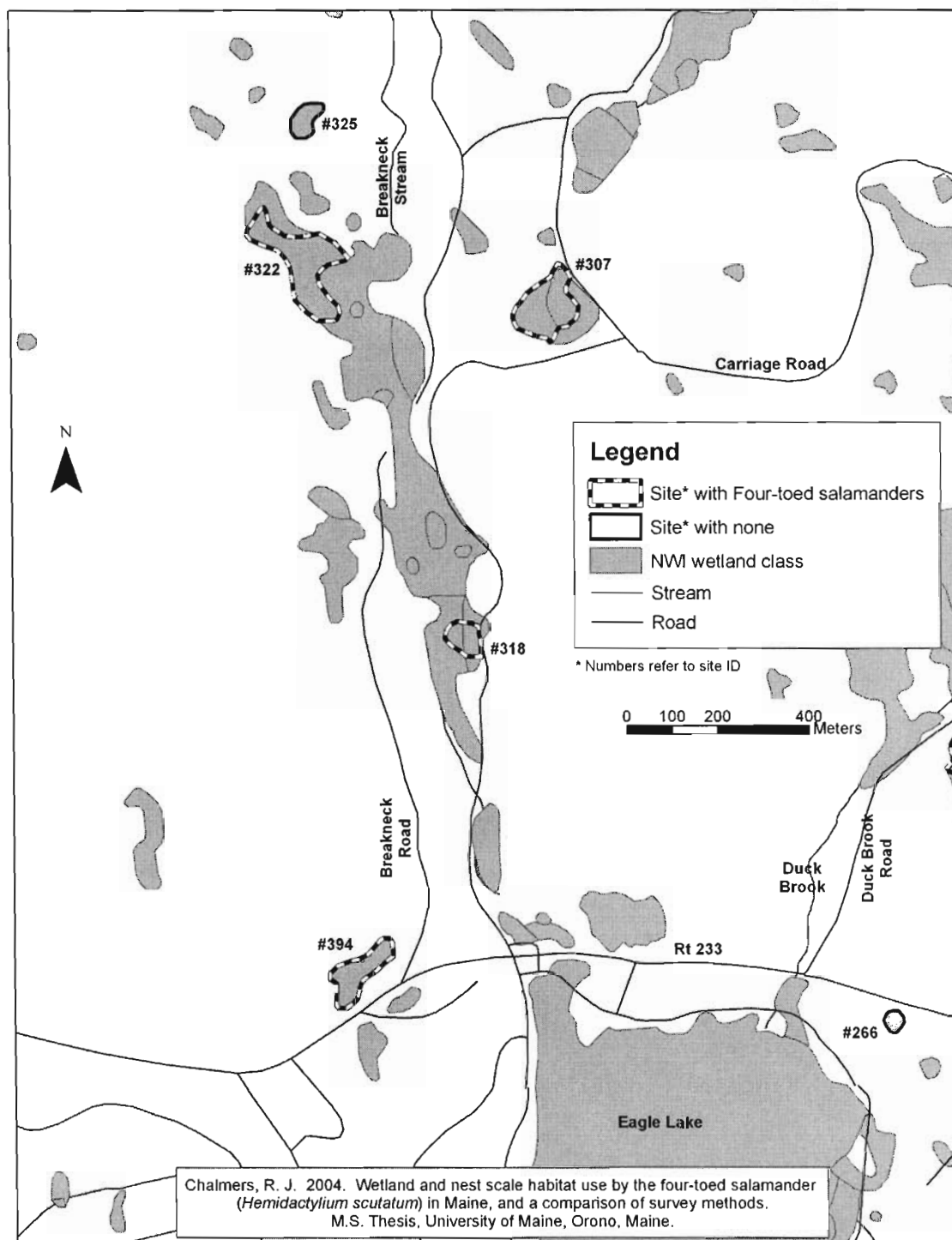


Figure B.10. Sites surveyed in Acadia National Park, Richardson Brook region.

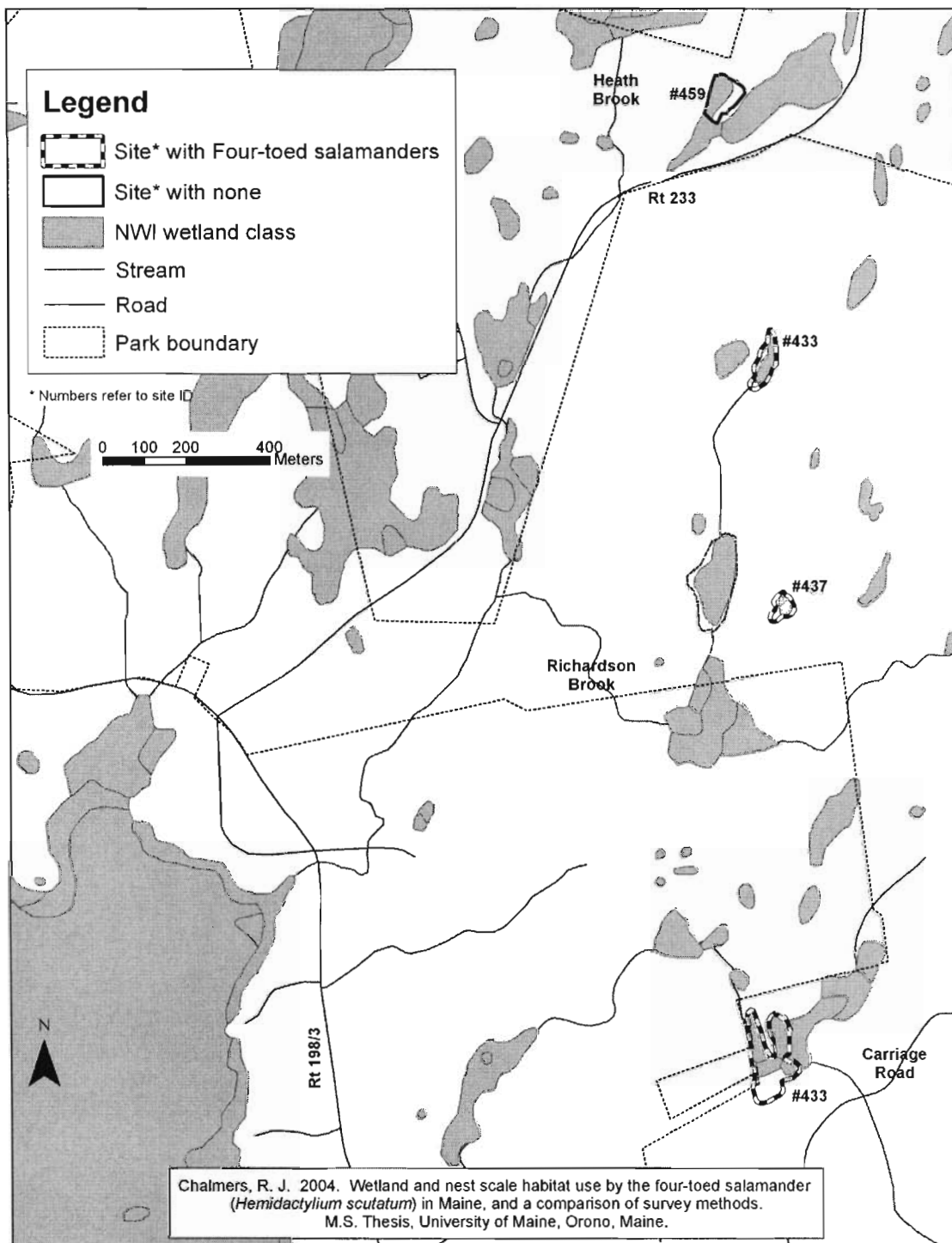


Figure B.11. Sites surveyed in Acadia National Park, Jordan Pond region.

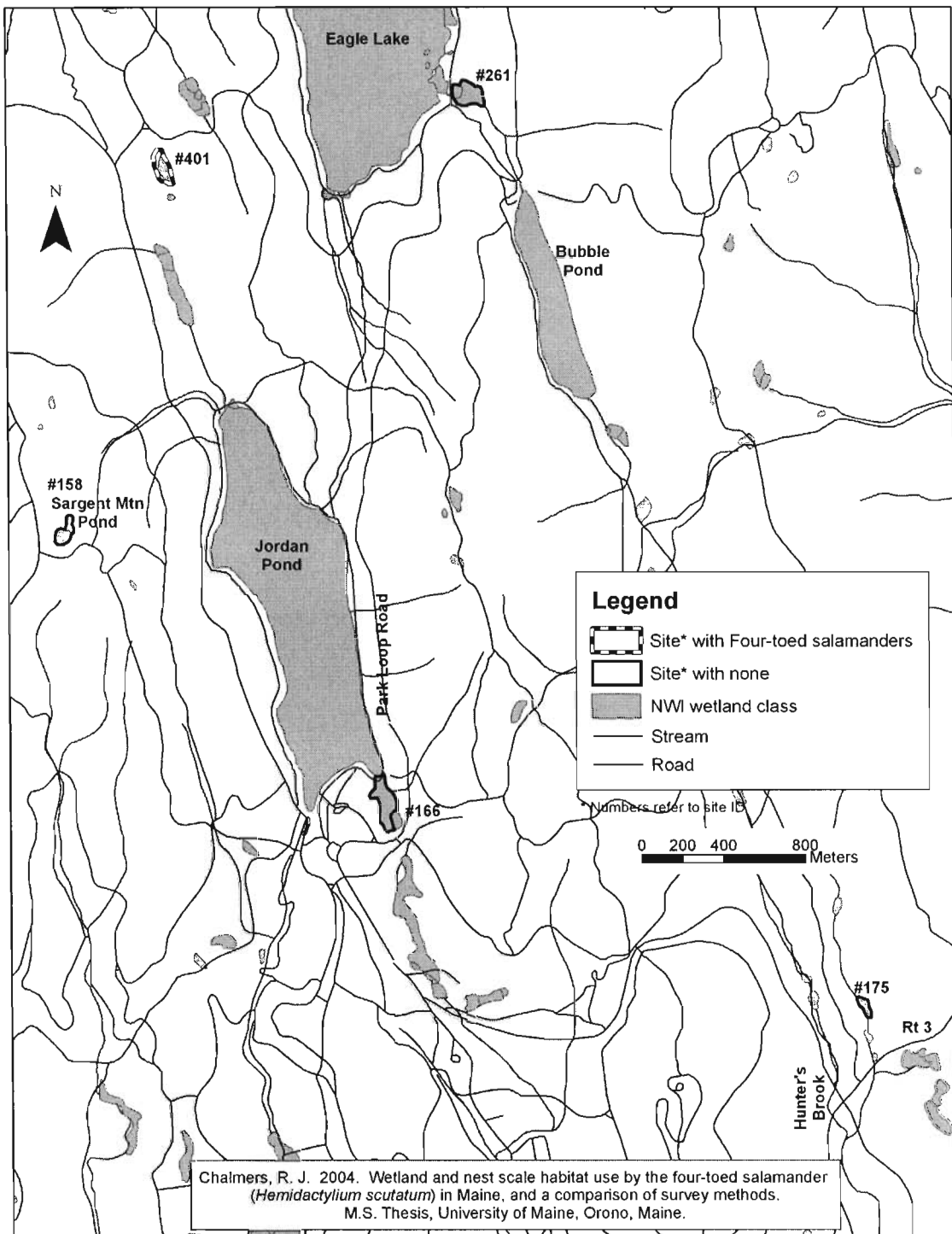


Figure B.12. Sites surveyed in Acadia National Park, Champlain Mountain region.

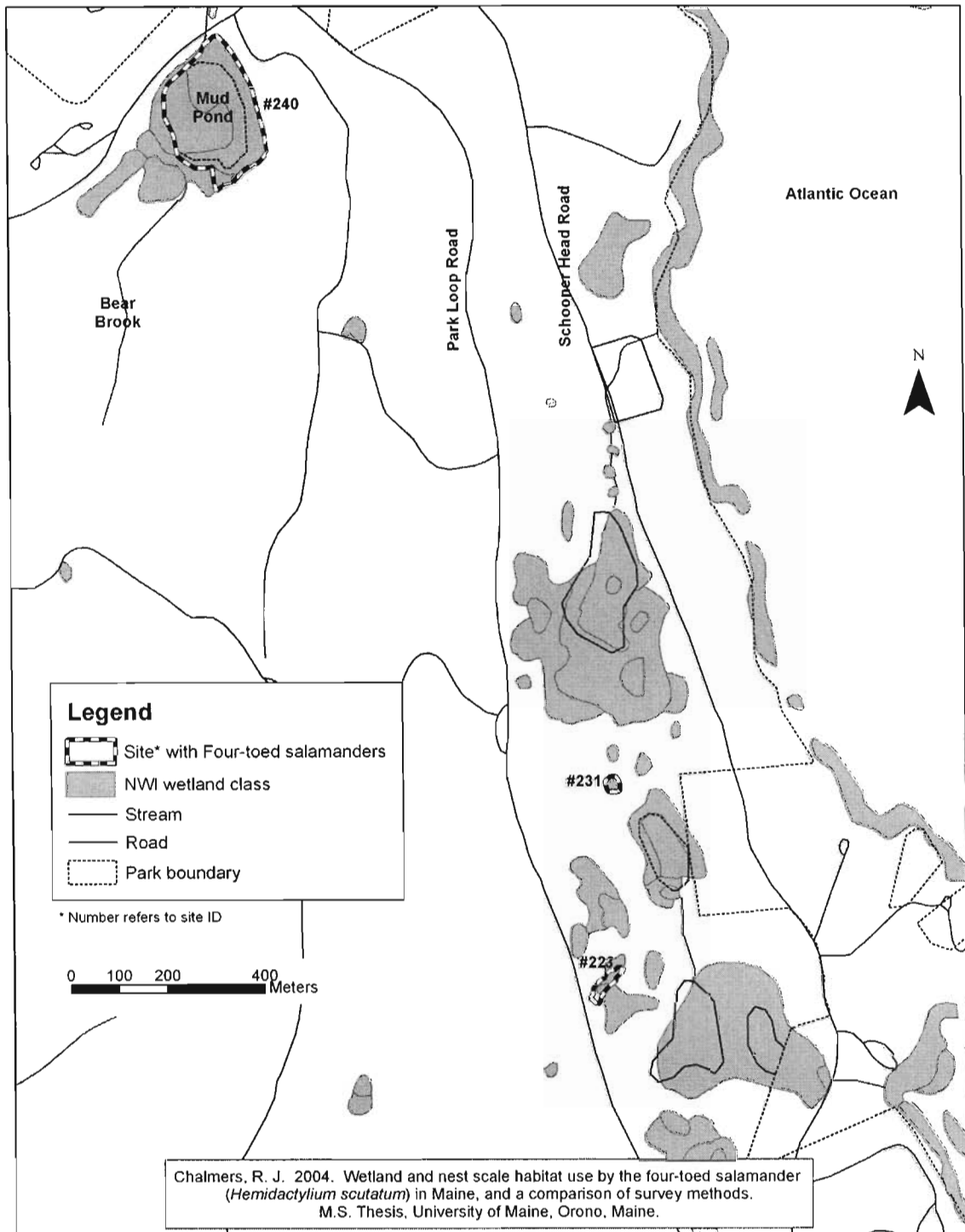


Figure B.13. Sites surveyed in University of Maine Demeritt Forest.

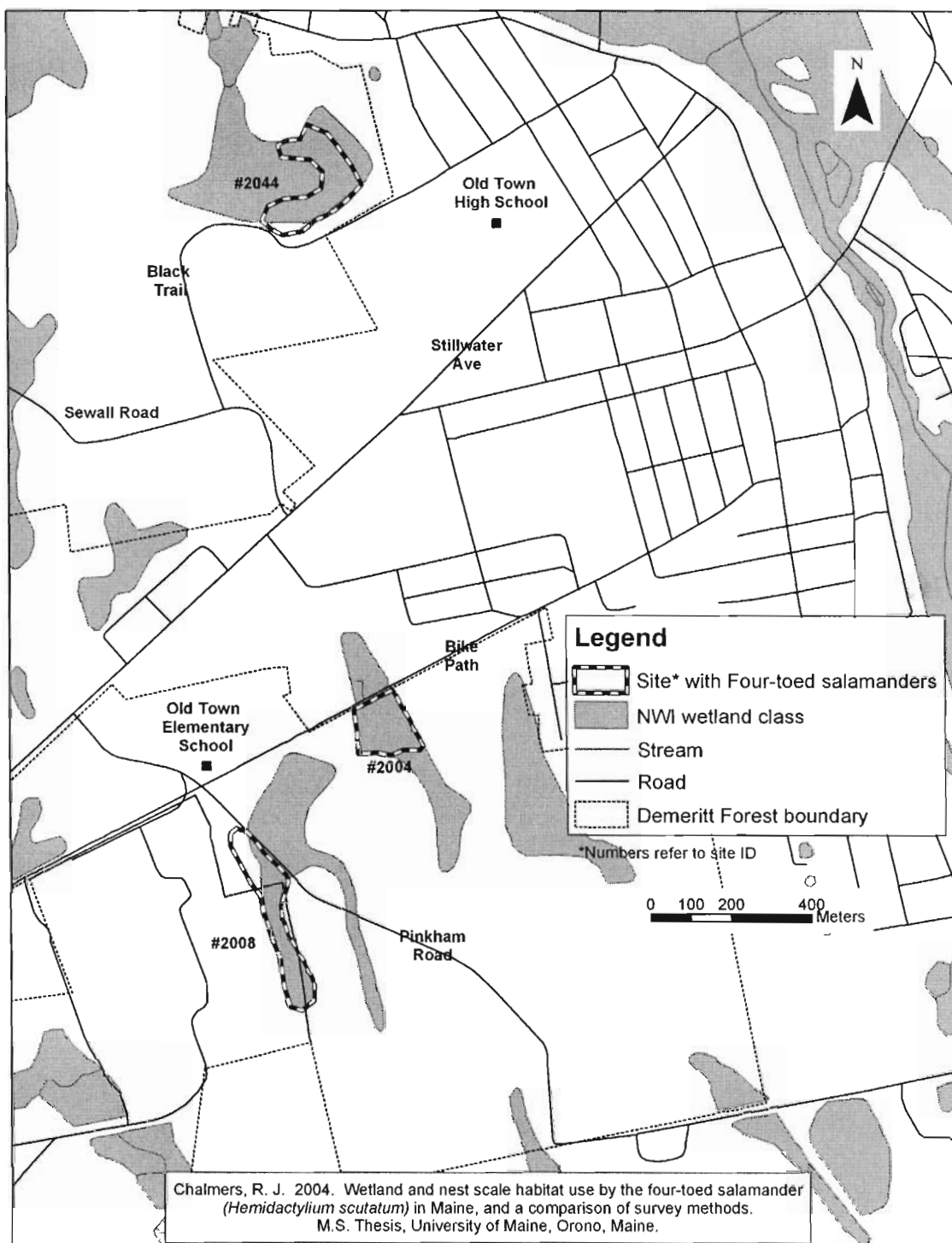


Figure B.14. Sites surveyed in University of Maine Foundation Penobscot Experimental Forest.

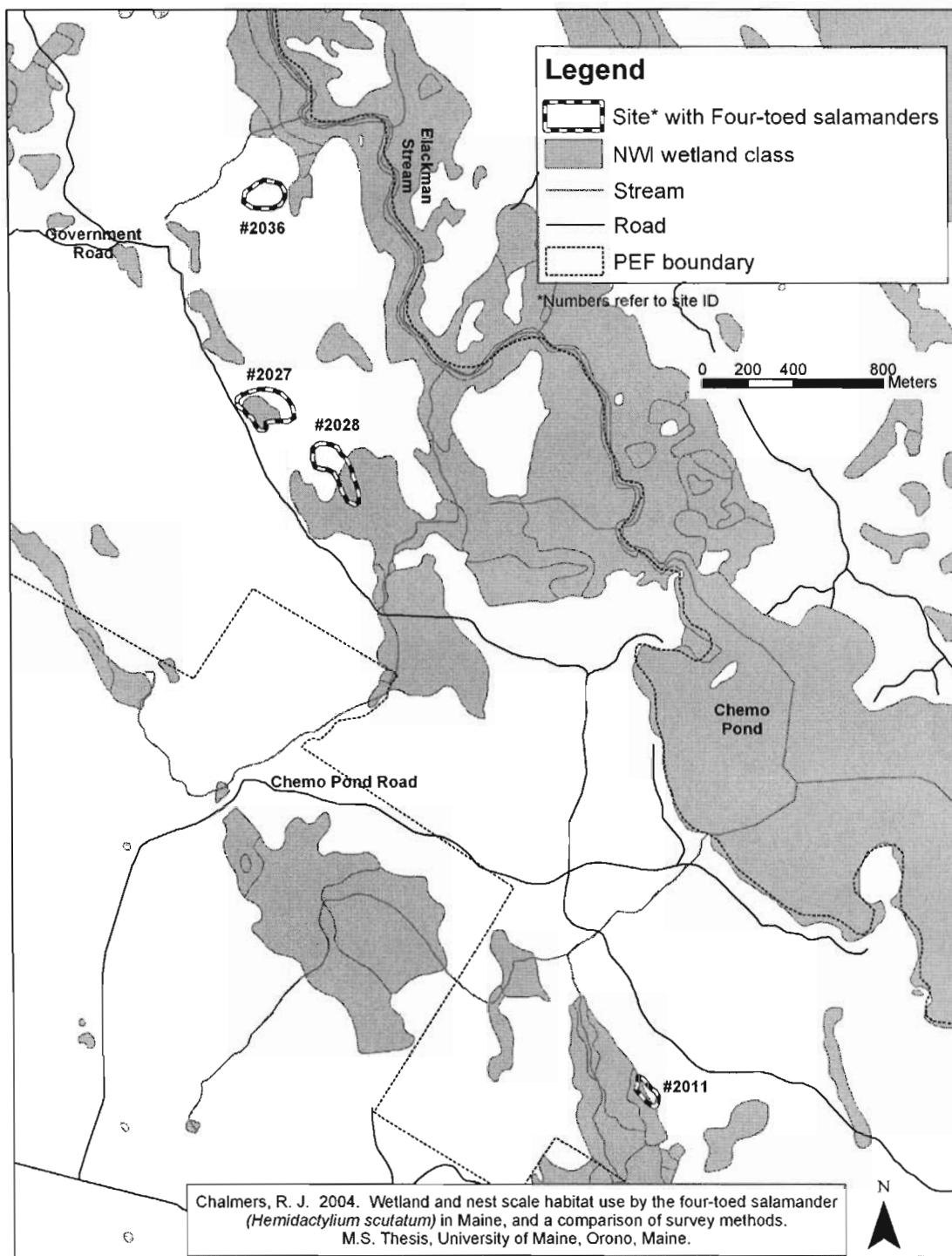


Figure B.15. Sites surveyed in USDA Forest Service Northeastern Research Station Massabesic Experimental Forest, North Unit, north region.

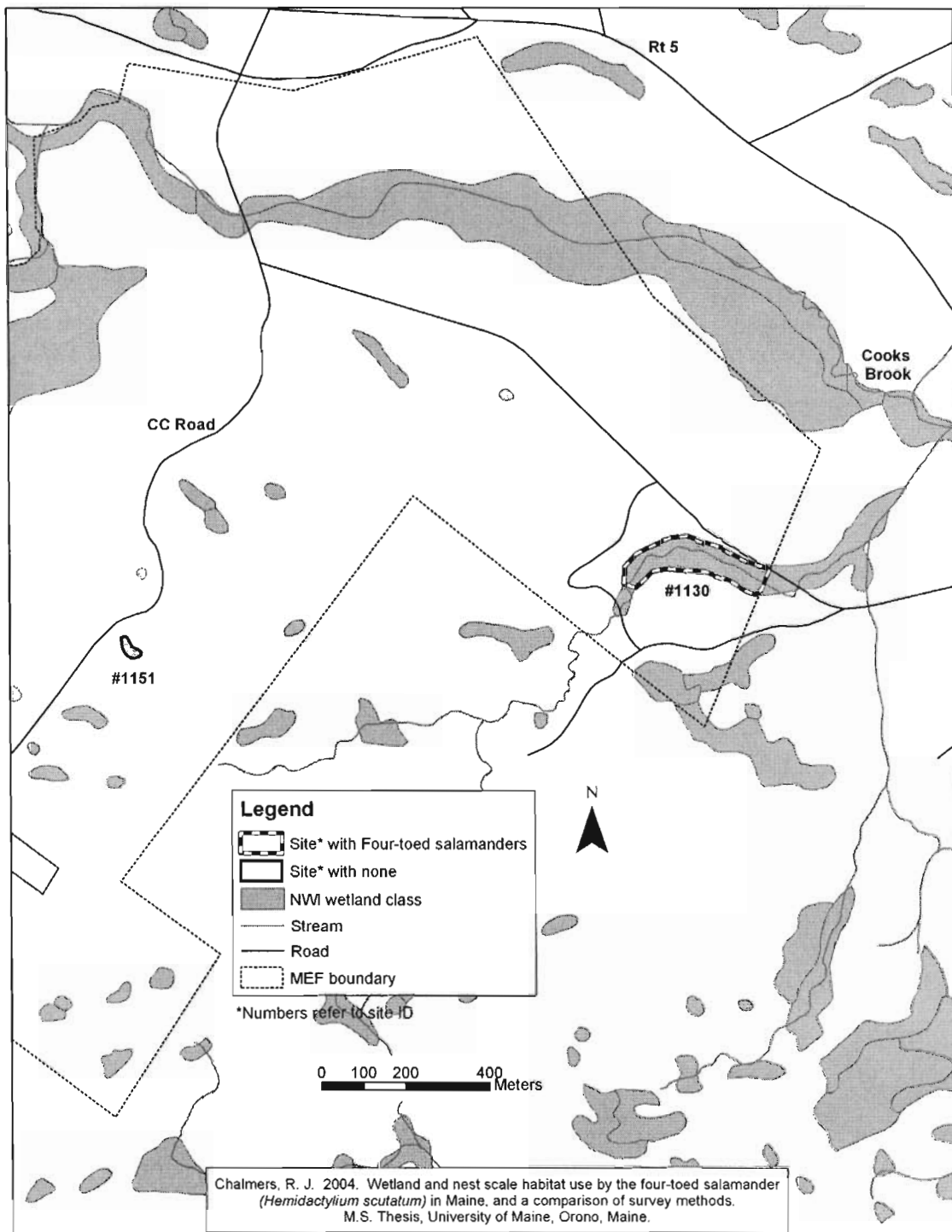


Figure B.16. Sites surveyed in USDA Forest Service Northeastern Research Station  
Massabesic Experimental Forest, North Unit, Jellerson Road region.

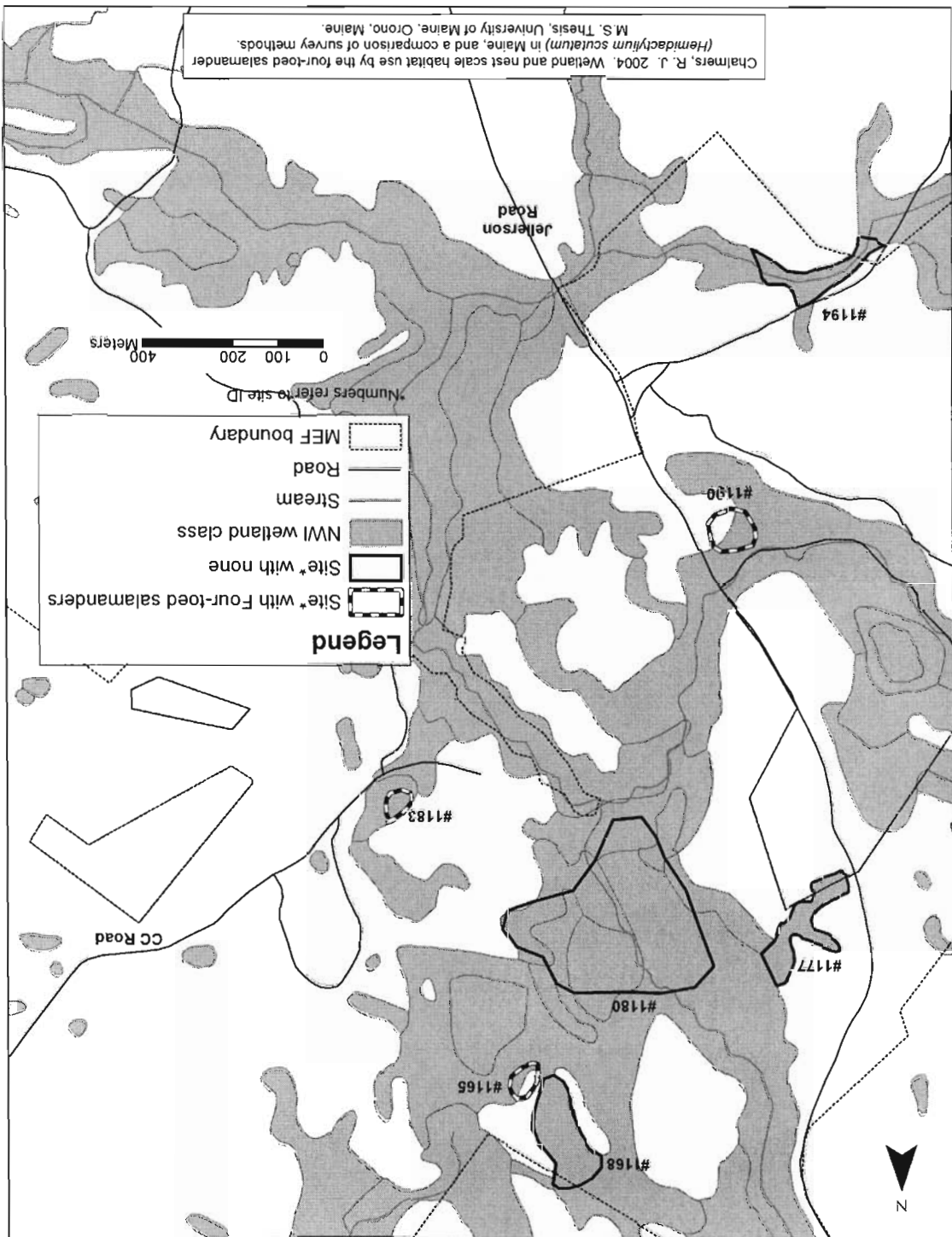


Figure B.17. Sites surveyed in USDA Forest Service Northeastern Research Station  
Massabesic Experimental Forest, South Unit.

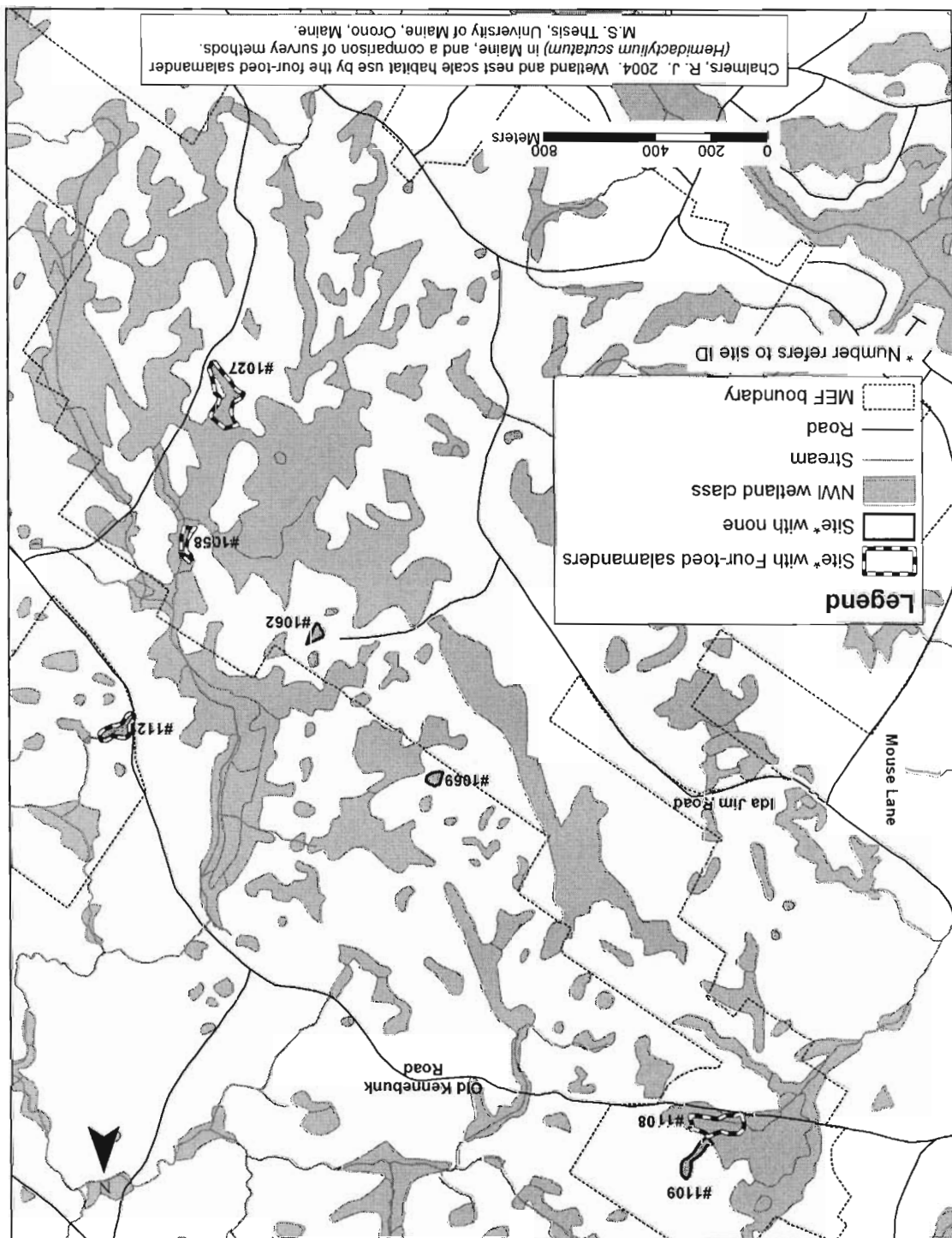
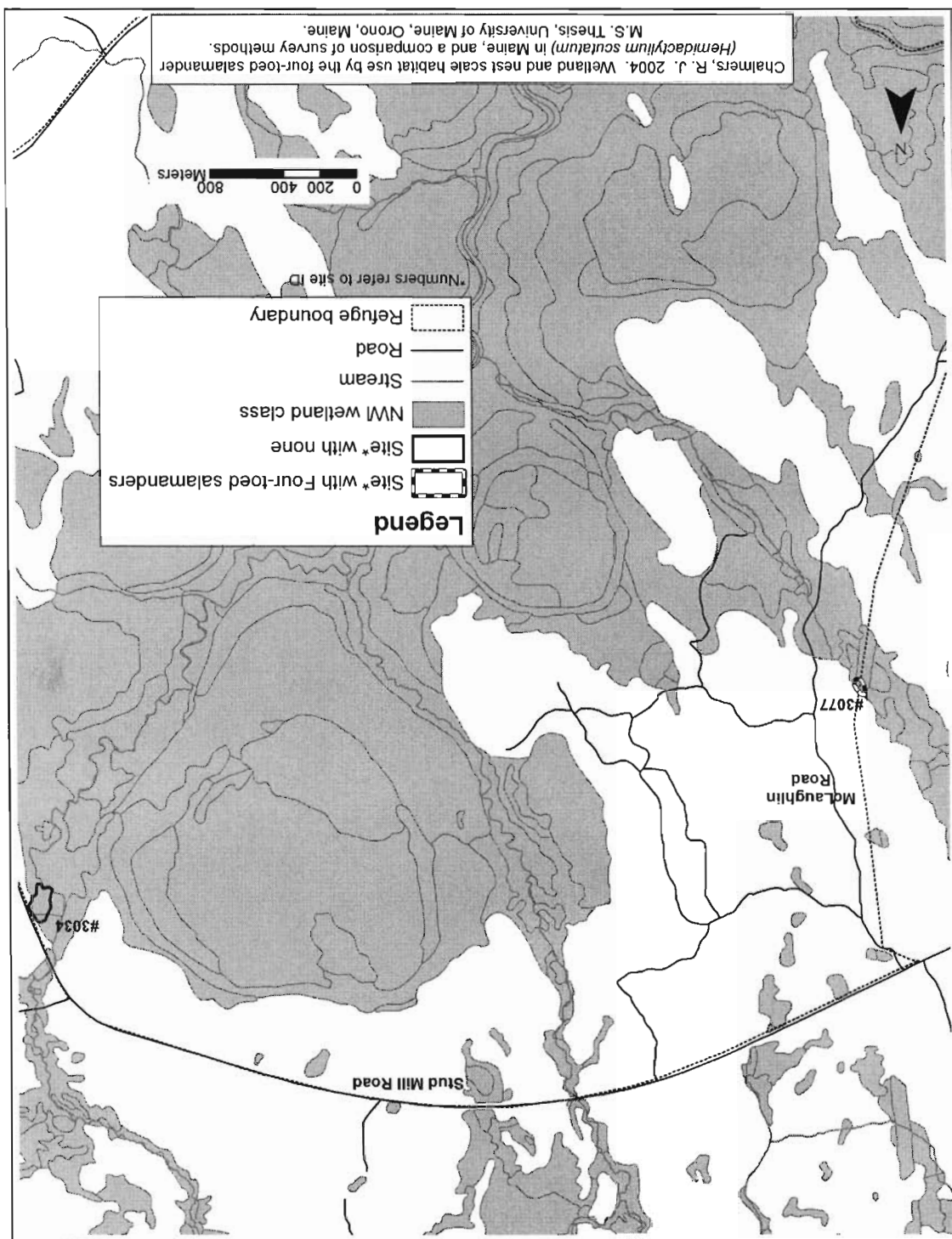


Figure B.18. Sites surveyed in USFWS Sunkhaze Meadows National Wildlife Refuge.



**APPENDIX C. UTM coordinates (NAD 1983 Datum, Zone 19) of study sites and additional locations at which *H. scutatum* have been found.**

Table C.1. Count of *H. scutatum* nests and UTM coordinates within each study wetland ( $n = 67$ ).

Year	Land unit	Figure # of map	Site ID	<i>H. scutatum</i> nest count	X	Y	Error
2002	ANP	4	17	0	0547723	4908806	16.2
2002	ANP	4	18	13	0547789	4908869	22
2002	ANP	4	20	0	0548266	4908994	19
2002	ANP	4	21	0	0548282	4908921	
2002	ANP	3	43	2	0548563	4906171	0
2002	ANP	2	82	0	0550859	4902648	31.7
2002	ANP	1	104	0	0554403	4900122	17
2002	ANP	1	105	0	0554501	4900301	16
2002	ANP	1	121	0	0554518	4897622	
2002	ANP	1	122	0	0554834	4897983	17.9
2002	ANP	1	128	0	0554260	4898263	
2002	ANP	1	136	0	0555690	4899097	16.6
2002	ANP	2	138	0	0551447	4904804	38.5
2002	ANP	11	158	0	0558224	4909241	
2002	ANP	11	166	0	0559803	4908049	16.7
2002	ANP	11	175	0	0562191	4906901	26.4
2002	ANP	12	223	11	0564931	4910448	26
2002	ANP	12	231	5	0564960	4910876	
2002	ANP	12	240	5	0564134	4912449	
2002	ANP	11	261	0	0560247	4911494	
2002	ANP	7, 9	266	0	0560330	4913972	23.6
2002	ANP	6	276	0	0561414	4915612	26
2002	ANP	7	282	7	0560496	4914570	15
2002	ANP	5	294	7	0560484	4917133	14.7
2002	ANP	5	297	7	0560104	4916931	15.1
2002	ANP	5	299	0	0560029	4916731	54.8
2002	ANP	9	307	5	0559623	4915631	
2002	ANP	9	318	2	0559375	4914823	15.8
2002	ANP	9	322	5	0559108	4915667	13
2002	ANP	9	325	0	0559036	4915982	17.3
2003	ANP	8	347	0	0558376	4917858	14
2003	ANP	8	351	1	0558502	4917283	13.4
2003	ANP	8	355	0	0559061	4917725	18.4
2003	ANP	8	368	1	0558605	4916480	20
2003	ANP	8	380	0	0557548	4917282	1.4
2003	ANP	9	394	3	0559183	4914087	4.8
2003	ANP	11	401	4	0558749	4911131	

Table C.1. continued

Year	Land unit	Map figure #	Site ID	<i>H. scutatum</i> nest count	X	Y	Error
2003	ANP	10	433	33	0556499	4913313	23.8
2003	ANP	10	437	2	0556535	4912721	21.9
2003	ANP	10	443	10	0556560	4911618	29.5
2003	ANP	10	459	0	0556455	4914001	
2003	ANP	7	466	7	0560560	4914742	7.1
2003	MEF S	17	1027	3	0365168	4811005	
2003	MEF S	17	1058	3	0365290	4811602	18
2003	MEF S	17	1062	0	0364789	4811978	20.1
2003	MEF S	17	1069	0	0364257	4812459	25.3
2003	MEF S	17	1108	6	0363483	4813711	14
2003	MEF S	17	1109	0	0363527	4813897	16
2003	MEF S	17	1121	3	0365523	4812257	22.6
2003	MEF N	15	1130	5	0368549	4824138	25.9
2003	MEF N	15	1151	0	0367085	4823947	
2003	MEF N	16	1165	1	0365806	4823915	22.2
2003	MEF N	16	1168	0	0365679	4824083	20.7
2003	MEF N	16	1177	0	0365156	4823517	23.8
2003	MEF N	16	1180	0	0365576	4823403	21.5
2003	MEF N	16	1183	13	0366124	4823326	18
2003	MEF N	16	1190	6	0365393	4822717	26.6
2003	MEF N	16	1194	0	0365162	4822136	16.6
2003	DF	13	2004	7	0526937	4974719	21
2003	DF	13	2008	2	0526628	4974135	33.3
2003	DF	13	2044	5	0526646	4974979	22.6
2003	PEF	14	2011	1	0531957	4962777	21.2
2003	PEF	14	2027	1	0530188	4965870	
2003	PEF	14	2028	4	0530565	4954621	16.4
2003	PEF	14	2036	5	0530296	4966731	19.2
2003	SMNWR	18	3034	0	0537043	4984604	18.5
2003	SMNWR	18	3077	2	0532496	4983368	13.8

Table C.2. Locations and count of *H. scutatum* detected on roads at night or in wetlands other than study site wetlands.

Date	Region	Site description	<i>H. scutatum</i> count	UTM		
				X	Y	Error
4/21/2000	ANP	Duck Brook Road	4 adults on road, 10 tracks	0560564	4914726	5.6
				0560668	4914903	4.3
				0560673	4914920	5.3
5/31/2001	ANP	Witch Hole Pond, E shore	2 juveniles in wetland	0560297	4916807	16.1
5/28/2001	ANP	Oak Point Road	1 adult on road	0551473	4912873	4.8
6/5/2001	ANP	Ripple Pond, SW shore	1 nest	0551440	4911144	≈ 15
6/5/2001	ANP	Study site ID 17	1 adult in wetland, no nest	0547710	4908812	≈ 15
4/8/2002	ANP	Duck Brook Road	3 adults on road	0560564	4914726	5.6
5/21/2003	ANP	Behind study site ID 466	7 nests	0560556	4914759	≈ 5
6/1/2002	Baxter	Wetland NE of S entrance gate	1 nest	0508308	5075259	≈ 100
5/2/2004	DF	Bike Path by Witter Farm Road	1 adult on road	0526210	4973767	≈ 50
5/3/2004	DF	Bike Path by Witter Farm Road	1 adult on road	0526210	4973767	≈ 50

## BIOGRAPHY OF THE AUTHOR

Rebecca Jean Chalmers was born in Baltimore, Maryland in 1975. She graduated from Howard High School in Ellicott City, Maryland in 1993. Upon completing high school, she traveled, interned with an Appalachian naturalist, and studied photography at the Maryland Institute College of Art. She attended the consensus-run Audubon Expedition Institute of Lesley University for a semester in South Dakota and Montana. Ms. Chalmers was an NSF Research Experience for Undergraduates fellow at Mountain Lake Biological Station, Virginia, during 1997. Rebecca received a Bachelor of Arts in Biology, high honors, from Marlboro College, Vermont in 1998.

Rebecca worked as a researcher for the Amphibian Research and Monitoring Initiative in The Great Smoky Mountains and Acadia National Parks. During this period, she published one paper of her original research (Chalmers, R. J. and S. Droege. 2002. Leaf litter bags as an index to populations of northern two-lined salamanders (*Eurycea bislineata*). *Wildlife Society Bulletin*, 30:71-74). Rebecca worked as an ecology instructor with the Appalachian Mountain Club, an assistant botanist with The Maine Forest Biodiversity Project, and an Air and Water Biological Technician with Acadia National Park.

Ms. Chalmers entered the Department of Wildlife Ecology at the University of Maine in 2001 to work with Dr. Cynthia Loftin. She studied wetland ecology, statistics, and GIS. She presented her research at national and regional meetings. Rebecca is a candidate for the Master of Science degree in Ecology and Environmental Science from The University of Maine in December, 2004.