Differences in eastern red-backed salamander (*Plethodon cinereus*) populations in hemlock-dominated and mixed deciduous forests in north-central Massachusetts

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Preface

This thesis consists of three chapters. The first chapter provides a background on the biology of eastern red-backed salamanders (*Plethodon cinereus* Green) and the habitat factors which affect terrestrial salamander populations. The unique structure and microenvironment of hemlock-dominated forests and the wildlife associated with this forest type as well as the threat to eastern hemlock (*Tsuga canadensis* (L.) Carr.) presented by the eastern hemlock woolly adelgid (*Adelges tsugae* Annand) is also discussed in this chapter. The chapter concludes with an overview of past work I have conducted assessing the relative abundance of *P. cinereus* at the Harvard Forest. The second chapter documents the research that was conducted for this thesis, and is intended as a stand-alone document. The third chapter explores in greater depth the results from this study, and examines areas which warrant further research.

CHAPTER 1

Introduction

Throughout eastern North America, an invasive insect, the hemlock woolly adelgid (*Adelges tsugae*) (henceforth "HWA"), has caused severe decline in the important late successional tree species, eastern hemlock (*Tsuga canadensis*). There is very little known about how the loss of this dominant species will impact associated wildlife. This study examines the relative abundance of an ecologically important forest organism, the eastern red-backed salamander (*Plethodon cinereus*) in hemlock-dominated forest and mixed deciduous forest. In this chapter I provide background on the basic biology of eastern red-backed salamanders, and discuss the factors which impact salamander distribution. The unique structure and microenvironment of hemlock-dominated forests and the wildlife associated with this forest type are discussed next. I then discuss the ecological effects of HWA which has caused severe decline in eastern hemlock throughout its range. I conclude this chapter by discussing my past work assessing the relative abundance of *P. cinereus* at the Harvard Forest, and by stating my hypotheses for this new study of the relative abundance of *P. cinereus* in north-central Massachusetts.

Eastern Red-backed Salamanders

Salamanders are vertebrates comprising the order Caudata in the class Amphibia (Duellman and Trueb 1986). All amphibians are ectotherms, and they are distinct from other vertebrates in that they possess two occipitial condyles (projections from the back of the skull), one or no sacral vertebrae, glandular skin, and a non-calcareous shell

(Duellman and Trueb 1986). Prominent tails, two pairs of legs roughly equal in size, four toes on the front feet, and five on the back feet, and no claws or external ear openings distinguish salamanders from other amphibian species (Petranka 1998). Salamanders account for 8.5% of the 4600 known living amphibian species. Of these 400 species, 127 occur in the United States. Salamander diversity is extremely high in the forests in the southeastern United States with seven families, nineteen genera, and seventy-five species occurring in this region. In contrast, eleven species of salamanders from four families and eight genera are found in Massachusetts. *Plethodon cinereus* is in the largest family of salamanders, the Plethodontidae, containing 27 genera and about 240 species. All salamanders in this family are lungless and respire through their skin and the upper lining of their mouth. In addition, plethodontids have nasolabial grooves extending from the margin of the upper lip to the lateral corner of each nare, which assist in the movement of chemicals from the substrate to the vomeronasal organ.

Although they are often overlooked due to their small size and cryptic behavior, salamanders are important components of forested ecosystems (Burton and Likens 1975a). At Hubbard Brook Experimental Forest in Coos County, New Hampshire terrestrial salamanders accounted for twice the biomass of breeding birds and the equivalent biomass of small mammals. *P. cinereus* was the dominant terrestrial salamander, accounting for 93.5% of the total biomass of salamanders, while three streamside species, two-lined salamander *(Eurycea bislineata* Green), dusky salamander (*Desmognathus fuscus* Green), and the northern spring salamander (*Gyrinophilus p. porphyriticus* Green) accounted for the remainder. Although they are often common in forests in New England which are within 1 km of suitable breeding habitat (Healey 1975;

Mathewson 2004), juvenile eastern red-spotted newts (*Notophthalmus v. viridescens*) were rare as the nearest potential breeding pond was greater than 3.5 km away.

The estimated density of *P. cinereus* in the northern hardwood forests in New Hampshire was 0.26 salamanders/m^2 (Burton and Likens 1975a). Estimates of the density of *P. cinereus* in other areas of its range include 0.21 salamanders/m^2 in Pennsylvania (Klein 1960), 0.89 salamanders/m^2 in Michigan (Heatwole 1962), 2.2 salamanders/m^2 and 2.8 salamanders/m^2 in Virginia (Jaeger 1980a; Mathis 1991b), and 0.56 salamanders/m^2 in Delaware (Rooney et al. 2000). In central Massachusetts, the average density of *P. cinereus* on the surface of the forest floor during the day was 0.13 salamanders/m^2 in the fall and 0.08 salamanders/m^2 in the spring (Mathewson 2004). Taub (1962) estimates that between 2% and 32% of the total population of *P. cinereus* is found on the surface of the soil during the day. This translates into estimates of between 0.41 salamanders/m^2 and 6.5 salamanders/m^2 in the fall, and 0.25 salamanders/m^2 and 5.0 salamanders/m^2 in the spring.

P. cinereus is a small, fully terrestrial salamander measuring between 6 cm and 12 cm in total length and weighing about one gram as an adult (Pough et al. 1987; Petranka 1998). *P. cinereus* has legs which are short relative to its body size, 18-20 costal grooves (parallel grooves along the side of the body), and a tail which is round in cross-section (Petranka 1998). There are four color morphs. The most common, the red-backed morph, has a broad orangish red to red dorsal stripe extending from the back of the head to the end of the tail, a black and white mottled venter, and dark sides. The second most common morph, the lead-backed morph, has an entirely dark body. There are also rare erythristic morphs which have an entirely bright red body and extremely rare albino morphs. In a study of fifty *P. cinereus* populations in New England, the frequency of the erythristic morph was greater than 10% in only three populations, and it never exceeded 20% (Lotter and Scott 1977). Interestingly, the percentage of lead-backed salamanders in a population (0%-33%) was found to be highly positively correlated with temperature in New England (Lotter and Scott 1977). More recent studies have found the lead-backed frequency to be 3% at the Harvard Forest and 40% at the Arnold Arboretum in Boston, Massachusetts (Mathewson 2004). Although uncommon, lead-backed frequencies of greater than 90% have been found in several populations of *P. cinereus* south of New England (Taub 1961; Highton 1962; Lotter and Scott 1977).

Secondary sexual characteristics of sexually active male *P. cinereus* include swollen nasolabial glands which enhance olfaction, glands on the tail (hedonic) and lower jaw (mental) which secrete chemicals that stimulate sexual activity, and elongated premaxillary teeth which have strongly curved cusps that are not found on any other *Plethodon* species (Petranka 1998). There is no sexual dimorphism in *P. cinereus* in terms of size or coloration. Males reproduce annually, while females have been found to breed biennially in Michigan, New York, Ohio, and Wisconsin. In a population in Connecticut, older females (snout-vent length (SVL) > 44cm) were found to reproduce every year (Lotter 1978).

Red-backed salamanders are terrestrial breeders, nesting in moist locations under rocks and logs and in subsurface retreats (Lynn and Dent 1941; Ng and Wilbur 1995). Females in Cape Cod, Massachusetts oviposit between June 18th and July 20th, most commonly in decaying pine logs (Lynn and Dent 1941). Females oviposit between 3-14 eggs in grapelike clusters, and stay with the eggs during a 6-9 week incubation period

(Ng and Wilbur 1995; Petranka 1998). Females defend their egg masses from various predators including conspecifics, other species of salamanders, ringneck snakes (*Diadophis punctatus* L.), and arthropods (Highton and Savage 1961; Forester 1979; Ng and Wilbur 1995). By keeping in constant contact with egg masses females keep eggs moist, and may also help prevent fungal infections through skin secretions (Heatwole 1961; Ng and Wilbur 1995). While brooding, females do not actively forage and only take prey opportunistically (Ng and Wilbur 1995).

Hatchlings are found abroad approximately two to three weeks after hatching (Sayler 1966). The smallest *P. cinereus* observed in Cunningham Falls, Maryland was observed in September and had an SVL of 14 mm (Sayler 1966). The growth rate of *P. cinereus* is slow between September and April due likely to low temperatures and a lack of available food (Sayler 1966). The greatest period of growth occurs between April and September in the first year with an average increase of 7.4 mm occurring during this period. Growth rates between April and September of the second year are considerably lower averaging about 1.5 mm. Individuals become sexually mature at the end of this second year (Blanchard 1928; Burger 1935; Sayler 1966). In a population of *P. cinereus* in Maryland 38% of salamanders with an SVL of 35mm, 64% of those with an SVL of 36mm, and 84% of those with an SVL of 37mm were found to be mature (Sayler 1966).

The size of the average home range of *P. cinereus* in northern Michigan is approximately 13 m^2 for males and juveniles and 24 m^2 for females (Kleeberger and Werner 1982). Home ranges were typically linear reflecting the reliance of *P. cinereus* on decaying logs which provide food, protection, and nesting habitat. The average distance traveled in a day by *P. cinereus* was 0.43 m; however, on rainy days individuals frequently moved further than 1 m.

Adult *P. cinereus* are able to efficiently forage for soil invertebrates which are too small for birds and mammals, the smallest of which have a body mass which is at least 20 times greater than that of *P. cinereus* (Pough et al. 1987). It is estimated that salamanders ingest one complete turnover of the standing crop of soil fauna per year (Hairston 1987; Wyman 1998). In addition, salamanders are extremely efficient at converting ingested prey into new biomass (Burton and Likens 1975b). While birds convert 2% of the food they consume into new biomass, salamanders convert 60%, enabling them to produce more new tissue than bird populations (Burton and Likens 1975b). Crump (1979) hypothesizes and Bobka et al. (1981) concur that assimilation efficiencies are so high in *P. cinereus* because prey is frequently unavailable during dry periods when *P. cinereus* cannot forage freely and must retreat to moist locations (Jaeger 1972).

Red-backs forage in the leaf litter and under cover objects (Burton 1976). In addition, on warm, wet nights, *P. cinereus* forage on the surface of the soil, and will also climb plants to forage for homopterans and hemipterans (Burton 1976; Jaeger 1978). *P. cinereus* use visual cues when foraging for motile prey, but they are also able to rely exclusively on chemical cues when foraging for non-motile prey (David and Jaeger 1981). Mites make a significant numerical contribution to the diet of *P. cinereus* as 82.5% of individuals (n=200) captured in the summer at Hubbard Brook Experimental Forest had mites in their stomach (Burton 1976). Mites contribute only 5% of the overall weight of prey, however. More important than mites in percentage of weight of prey were two-winged flies (Diptera) (30.2%), beetles (Coleoptera) (22.2%), butterflies (Lepidoptera) (8.4%), Hemiptera (7.7%), and spiders (6.9%) (Araneida). Immature forms of these groups were extremely important, accounting for 59% of the overall weight of prey. While ants only contributed 1.9% of the weight of prey at Hubbard Brook, they were the most important prey item in Ithaca, New York accounting for 28.5% of weight of prey (Hamilton 1932). Ants were also found to be the most important prey item for a *P. cinereus* population in Delaware, accounting for 59% of weight of prey (Rooney et al. 2000).

There appears to be little competition for food resources between *P. cinereus* and the other four species of salamanders found at Hubbard Brook due primarily to a gradient in size which leads to a corresponding gradient in size of prey taken (Burton 1976). The average wet weight of *P. cinereus* (0.63g) was lowest among all salamander species which included *E. bislineata*, juvenile eastern red-spotted newt (*Notophthalmus v. viridescens* Rafinesque), *D. fuscus,*, and *G. p. porphyriticus*. The species which is closest in size to *P. cinereus*, *E. bislineata* (0.67g), is primarily found in and around streams and seeps, but it is also found a few meters away in fully terrestrial situations. In these areas where the two species overlap, *E. bislineata* is found to eat more collembolans and snails than *P. cinereus*. Interestingly, *P. cinereus* also consume significantly fewer snails than the only other terrestrial salamander found at Hubbard Brook, juvenile *N. v. viridescens* (2.4% vs. 59.7%), which had an average weight of 1.45 g.

The tissue of *P. cinereus* is very high in protein, making them important prey to many higher vertebrates (Burton and Likens 1975b; Petranka 1998). Pough et al. (1987) speculate that the numerous anti-predator behaviors of *P. cinereus* suggest that it is an important prey for a number of avian and mammalian predators. Organisms observed in the field preying on *P. cinereus* include birds which forage in the leaf litter such as hermit thrush (*Catharus guttatus* Pallas), American robin (*Turdus migratorius* L.), and wild turkey (*Meleagris gallopavo* L.) (Coker 1931; Fenster 1996; Eaton 1992). On one quarter of their visits to the nest *C. guttatus* were observed feeding salamanders to their young (Coker 1931). *P. cinereus* also contributes significantly to the diet of garter snakes (*Thamnophis sirtalis* L.) and ringneck snakes (*Diadophis punctatus* L.) (Uhler 1939). In the lab, short-tailed shrews (*Blarina brevicauda* Say) have been found to prey on *P. cinereus*, although less frequently than on Allegheny mountain dusky salamander (*Desmognathus ochrophaeus* Cope) (Brodie et al. 1979).

Experimental manipulations using enclosures suggest that predation by *P. cinereus* plays a role in controlling invertebrate community composition (Wyman 1998; Rooney et. al. 2000). A study of paired field enclosures in which salamander density was either zero salamanders/m^2 or four salamanders/m^2 found that, contrary to the authors' expectations, the relative abundance of the ecologically important group of arthropods, the Collembola (springtails), was higher in enclosures containing salamanders (Rooney et al. 2000). The authors of this study propose that salamanders may be indirectly causing an increase in the relative abundance of Collembola by preying on the large invertebrates which are their predators, such as ants, although the abundance of ants was not found to be impacted by the abundance of *P. cinereus* (Rooney et al. 2000)

P. cinereus may also influence ecosystem function such as the rate at which leaf litter decomposes (Wyman 1998). Enclosures containing salamanders were found to have decomposition rates between 11% and 17% lower than enclosures without salamanders (Wyman 1998). This may be explained by a lower abundance of key leaf fragmenters, such as millipedes, mollusks, and insect larvae in enclosures containing *P.*

cinereus (Wyman 1998). It has also been hypothesized that the abundance of *P. cinereus* may be positively correlated with decomposition rates because predation by terrestrial salamanders causes an increase in the diversity of detritivores making decomposition more efficient (Burton and Likens 1975b), and/or a decrease in the abundance of organisms which feed on the bacteria and fungi that account for the majority of decomposition (Hairston 1987). However, the only available evidence suggests that higher *P. cinereus* density leads to lower decomposition rates (Wyman 1998).

Habitat Factors Influencing the Relative Abundance of Terrestrial Salamanders

This section focuses on the numerous direct and indirect habitat factors which have been found to influence the relative abundance of *P. cinereus*. There are many other factors which also impact the relative abundance of populations including external factors, such as the abundance of competitors, predators and prey, and internal population factors such as birth, mortality, and migration rates. Some of the direct habitat factors which influence the relative abundance of terrestrial salamanders include soil moisture (Heatwole 1962; Feder 1983; Wyman and Hawksley-Lescault 1987; Grover 1998), soil temperature (Bobka et al. 1981), soil pH (Wyman and Hawksley-Lescault 1987; Frisbie and Wyman 1991; Wyman and Jancola 1992), and volume of coarse woody debris (CWD) (Grover 1998). Differences in the relative abundance of *P. cinereus* can also be explained by indirect factors which determine these environmental and structural qualities such as land-use history (Harpole and Haas 1999; Brooks 2001; Hicks and Pearson 2003) stand age (Welsh and Lind 1988; Dupuis et al. 1995; Ford et al 2002), and forest type (DeGraaf and Rudis 1990; Wyman and Jancola 1992).

As a lungless salamander which respires through its skin and must remain moist to breathe, *P. cinereus*, not surprisingly, prefers cool, moist microhabitats (Feder 1983). In the range of soil temperatures in which *P. cinereus* normally forages, higher temperatures result in lower assimilation efficiency rates and higher metabolic demands (Bobka et al. 1981). Taub (1961) found the temperatures at which *P. cinereus* were most commonly found on the surface of the forest floor to be between 5°C and 25°C. *P. cinereus* were rarely found when temperatures were below 4°C, presumably seeking warmer conditions deeper in the soil (Taub 1961). Moisture levels also have an important effect on the vertical distribution of *P. cinereus* with animals retreating deeper in the soil under drier conditions (Heatwole 1962).

Another important factor which has been found to impact the distribution of *P. cinereus* is soil pH (Wyman and Hawksley-Lescault 1987; Frisbie and Wyman 1991; Wyman and Jancola 1992). In Albany County, New York the abundance of *P. cinereus* was found to be significantly lower in quadrats in which the soil pH was below 3.7 (Wyman and Jancola 1992). One potential reason for this is that low soil pH leads to elevated sodium efflux rates in *P. cinereus* resulting in lower water levels and reduced body mass (Frisbie and Wyman 1991). *P. cinereus* may also avoid soils with low pH because of high levels of aluminum or mercury ions (Frisbie and Wyman 1991). Soils with low pH may also contain fewer *P. cinereus* prey, as two species of isopods (*Oniscus assellus* and *Admadillium vulgare*) and one species of millipede (*Diploidulus* spp.) were found to have greater than 50% mortality when exposed to soils with a pH between 3.0 and 3.5 (Wyman and Hawksley-Lescault 1987).

Another important factor influencing the relative abundance of *P. cinereus* has been found to be density of cover objects (Grover 1998; Brooks 2001). In a study in which the density of cover objects was experimentally manipulated the abundance of adult and juvenile *P. cinereus* and the adjusted biomass of adult *P. cinereus* was found to be higher in plots with higher densities of cover objects (Grover 1998). The relative abundance of *P. cinereus* has also been found to be positively correlated with volume of coarse woody debris (CWD) in the field (Brooks 2001). In a study of twenty-five hemlock-hardwood stands, Tyrell and Crow (1994) found that total volume of coarse woody debris (CWD) was positively correlated with stand age suggesting that the relative abundance of *P. cinereus* might be higher in older stands with more CWD.

Several studies, mostly conducted on the west coast of North America, have found a positive relationship between stand age and the relative abundance of terrestrial salamanders (Welsh and Lind 1988; Dupuis et al. 1995; Ford et al 2002). In old-growth Douglas-fir (*Pseudotsuga menziesii* Franco)/hardwood stands (> 200 years old) the relative abundance of terrestrial salamanders was found to be significantly higher than in young *P. menziesii* stands/hardwood stands (< 100 years old) in northwestern California and southwestern Oregon (Welsh and Lind 1988). In addition, within mixed *P. menziesii*/western hemlock (*Tsuga heterephylla* Rafinesque) stands in central Vancouver Island, Canada the mean density of salamanders was found to be between three and six times greater in old-growth forests (age 330+ - 500+ years) than in mature second growth forests (age 54 – 72 years) (Dupuis et al. 1995). In a study of second-growth, *P. menziesii* forests in the Pacific Northwest, the oldest second-growth forests (rotation age: 50-70 years) had the highest amphibian species richness, total biomass, and total abundance (Aubry 2000). In cover-hardwood stands consisting of yellow-poplar

(*Liriodendron tulipifera* L.), northern red oak (*Quercus rubra* L.), and white oak (*Q. alba*), the relative abundance of terrestrial salamanders, especially *Desmognathus* spp., was found to be higher in stands that were greater than 85 years old than in younger stands (Ford et al. 2002).

Several studies have examined how prior land-use, particularly logging, which increases surface temperatures and creates drier conditions, impacts the relative abundance of *P. cinereus* (Pough et al. 1987; Harpole and Haas 1999; Brooks 2001). Not surprisingly, given the physiological requirement of salamanders for cool, moist habitat there is a good deal of evidence that suggests the relative abundance of salamanders is lower following not only clearcut timber harvesting (Ash 1988; Pough et al. 1987), but also less intense silvicultural treatments (Harpole and Haas 1999). Logging treatments which were found to lead to lower relative abundance of *P. cinereus* include "group selection" (trees removed in three groups representing 25% of total area of plot), "shelterwoods" (between 4 and 15 m^2 basal area (BA) per hectare left per plot), and "leave-tree" (3-4 m^2 BA and a maximum of 16 trees (diameter at breast height (dbh) > 30cm) retained per hectare) (Harpole and Haas 1999).

While logging has a negative effect on the relative abundance of *P. cinereus* in the short-term, populations do appear to recover over time (Pough et al. 1987; Brooks 2001). In a study of hemlock-dominated stands in north-central Connecticut and south-central Massachusetts in which pre-emptive salvage logging was conducted to remove overstory hemlock, the relative abundance of *P. cinereus* was higher in plots which had been least recently logged (1-7 years post-harvest) (Brooks 2001). However, the relative abundance of *P. cinereus* in logged plots was still lower than in unlogged plots (Brooks

2001). In Tompkins and Schuyler counties in New York the relative abundance of *P. cinereus* appears to return to pre-disturbance levels after about 60 years (Pough et al. 1987). No difference was found in the diversity or relative abundance of salamanders in abandoned farmland (land primarily used as pasture prior to 1943) versus second/third growth timber forests (land which had been logged twice since the late 1800s most recently between 1940 and 1960) in Buncombe County, North Carolina, although the relative abundance of salamanders was higher in historically undisturbed forest than in either of these two land-use categories (Hicks and Pearson 2003).

Few studies have quantitatively assessed the relative abundance of *P. cinereus* in different forest types. In the northernmost part of the White Mountains in New Hampshire, the relative abundance of *P. cinereus* was lower in balsam fir stands than in red maple or northern hardwood stands, probably due to the high acidity of the soil in balsam fir stands (pH = 2.4) (DeGraaf and Rudis 1992). Low soil pH is also believed to be the reason why the relative abundance of *P. cinereus* is lower in hemlock-dominated forests than beech-dominated forests in Albany County, New York (Wyman and Hawksley-Lescault 1987; Frisbie and Wyman 1991; Wyman and Jancola 1992). At the Harvard Forest, the relative abundance of *P. cinereus* was found to be higher in hemlock-dominated forests than mixed deciduous forests in three of four seasons (Mathewson in review).

Wildlife Habitat Associations in Hemlock-dominated Forests

The hemlock-dominated forest type is structurally unique from other forest types in New England and has a unique microenvironment which provides habitat for numerous wildlife species (Benzinger 1994b; Orwig and Foster 1998; Yamasaki et al. 2000). As a shade tolerant, late successional species, *T. canadensis* retains its lower branches and has dense foliage from the bottom to the top of the tree (Orwig and Foster 1998). This vertical complexity results in a dark, damp, cool microclimate on the forest floor (Benzinger 1994a; Mathewson in review; Hadley unpublished data) and a depauperate understory (Rogers 1980). In addition, as *T. canadensis* is a late-successional species hemlock-dominated forests are often older with potentially higher volumes of coarse woody debris (CWD) (Tyrell and Crow 1994).

The vertical complexity of hemlock-dominated forests provides foraging and nesting habitat for many species of breeding songbirds including black-throated green warbler (*Dendroica virens* Gmelin), solitary vireo (*Vireo solitarius* Wilson), blackburnian warbler (*Dendroica fuscus* Müller), ovenbird (*Seirus auracapillus* L.), black-capped chickadee (*Parus atricapillus* L.), winter wren (*Trogolodytes trogolodytes* L.), red-breasted nuthatch (*Sitta canadensis* L.) and hermit thrush (*Catharus guttatus* Pallas) (Benzinger 1994b; Yamasaki et al. 20000). At the Quabbin Reservation in central Massachusetts *D. virens, V. solitarius, and D. fusca* were strongly associated with hemlock-dominated forests (Garrett unpubl. 2002). In particular, *D. virens* was more abundant in hemlock-dominated stands than in hardwood or white pine stands. Acadian flycatcher (*Empidonax virescens* Vieillot) and Louisiana waterthrush (*Seiurus motacilla* Vieillot) were found almost exclusively at hemlock stream sites. Large predatory birds are also associated with hemlock-dominated stands including the northern goshawk (*Accipiter gentiles* L.) which is considered a "hemlock obligate" in New Jersey (Benzinger 1994b), and four species of owls, great horned (*Bubo virginianus* Gmelin), long-eared (*Asio otus* L.), northern saw-whet (*Aegolius acadicus* Gmelin), and barred (*Strix varia* Barton) (Yamasaki et al. 2000).

Hemlock-dominated forests also provide important habitat for wildlife in the winter (Yamasaki et al. 2000). White-winged crossbill (*Loxia leucoptera* Gmelin), red crossbill (*Loxia curvitostra* L.), pine siskin (*Carduelis pinus* Wilson), goldfinch (*Carduelis tristis* L.), and evening grosbeak (*Coccothraustres vespertinus* Cooper), forage for hemlock seeds in the winter (DeGraaf and Rudis 1986; Howe and Mossman 1995; Yamasaki et al. 2000). White-tailed deer (*Odocoileus virginianus* Boddaert) also use hemlock-dominated forests in the winter when snow depth is lower than in mixed deciduous forest (DeGraaf and Yamasaki 2001; Yamasaki et al. 2000). Hemlock-dominated forests provide important roosting habitat for ruffed grouse (*Bonasa umbellus* L.) (Yamasaki et al. 2000).

Another unique structural quality of hemlock-dominated forests is large downed logs as *T. canadensis* is shallow rooted and susceptible to blowdowns (Rogers 1978; Yamasaki et al. 2000). These large logs provide nesting sites for fisher (*Martes pennanti* Erxleben) and bobcat (*Lynx rufus* Schreber) (Yamasaki et al. 2000). Black bear (*Ursus americanus* Pallas) also uses hemlock-dominated forests, foraging in coarse woody debris for ants in the spring and in the winter using trees and logs as shelter (DeGraaf and Rudis 1986; Yamasaki et al. 2000). Twenty-three species of insectivores, hares and rodents use hemlock-dominated stands in the northeast and five species: snowshoe hare (*Lepus americanus* Erxleben), red squirrel (*Tamiasciurus hudsonicus* Erxleben), deer mouse (*Peromyscus maniculatus* Wagner), southern red-backed vole (*Clethrionomys gapperi* Vigors), and porcupine (*Erethizon dorsatum* L.), have been found to be strongly associated with *T. canadensis* as well (Yamasaki et al. 2000). Dense conifer understories found in regenerating patches within hemlock-dominated stands provide habitat for *L. americanus*, while large *T. canadensis* trees and downed logs provide critical *E. dorsatum* habitat (Yamasaki et al. 2000).

The loss of hemlock-dominated forests may cause biodiversity to increase at the stand level, but to decrease at the landscape level (Tingley et al. 2002). While avian species diversity was higher in hemlock-dominated forests infested with HWA than in healthy hemlock-dominated forest, the species which were found to be more abundant in healthy hemlock-dominated forest, *D. virens*, *E. virescens*, *D. fuscus*, and *C. guttatus*, were found exclusively in this forest type. This suggests that the loss of healthy hemlock forest will cause a decrease in overall avian species diversity across the landscape. It is also interesting that one of the species found to be significantly more abundant in HWA infested hemlock-dominated forests than in healthy hemlock-dominated forests is the brood parasite, brown-headed cowbird (*Molothrus ater* Boddaert), a species which can have a significant negative impact on the breeding success of passerines through a reduction in the numbers of birds fledged (Hersek et al. 2002). Hemlock-dominated forests also add to the diversity of ant communities across the landscape, as ecologically important *Formica* spp. appear to be absent from hemlock-dominated forests in Connecticut and Massachusetts (Ellison et al. 2005). The abundance and diversity of soil fauna was found to be higher in hemlock litter than in litter from mixed deciduous stands consisting of maple, beech, oak, ash, and birch in Saltonstall Ridge, Connecticut (Hartman 1977). Centipedes (class Chilopoda), mites and ticks (order Acarina), springtails (order Collembola), and spiders (order Araneae) were all more than five times more abundant in hemlock litter than mixed deciduous litter (Hartman 1977).

Very little is known concerning the relative abundance of amphibians in hemlock dominated forests. Several characteristics of hemlock-dominated forest including cooler temperatures (Benzinger 1994b; Mathewson in review), moister soils (Hadley unpubl.), potentially higher volumes of CWD (Tyrell and Crow 1994), and a higher abundance of invertebrate prey (Hartman 1977), suggest that the relative abundance of *P. cinereus* might be higher in this forest type. However, if soil pH is below the level which *P. cinereus* can tolerate these traits obviously become less important (Wyman and Jancola 1992).

Hemlock Woolly Adelgid

Throughout the twentieth century several dominant tree species, such as American beech (*Fagus grandifolia* Ehrh.), American chestnut (*Castanea dentata* (Marshall) Borkh.), and American elm (*Ulmus americana* L.), suffered severe declines in the northeastern United States due to exotic pests and pathogens (Orwig 2002). Currently, the invasive aphid-like insect pest, HWA, threatens another dominant late-successional tree species, *T. canadensis*, throughout its range (Orwig and Foster 1998; Orwig 2002). This insect pest is believed to have been first introduced in Virginia in the 1950s (Souto et al. 1996). HWA been able to spread rapidly (approximately 30 km year^{-1}) due its small size and woolly filaments found on egg masses and other life stages which aid in its dispersal by the wind, birds, deer, and humans (McClure 1987; McClure 1990). In addition, HWA has a polymorphic life cycle and completes two generations in a year (McClure 1987).

HWA has caused widespread mortality of *T. canadensis* from North Carolina to New Hampshire (Orwig 2002). HWA is now found in 50% of the towns in Massachusetts, although overstory mortality is still low in most stands except along the coast and in the south central portion of the state (Orwig et al. unpublished data). In stands in Connecticut, where HWA was first introduced in 1985, overstory mortality rates have been as high as 99% (Orwig and Foster 1998). It is not completely clear how HWA kills hemlock trees, but it is known that the insect feeds on the parenchyma cells in hemlock needles, killing trees of all ages usually within 4-10 years (McClure 1990; Young et al. 1995). Neither stand nor landscape variables exert control over the susceptibility of hemlock stands to infestation (Orwig et al. 2002).

The pre-emptive removal of *T. canadensis* by logging, often accompanied by the removal of other more economically valuable species, such as red oak (*Quercus rubra* L.) and white pine (*Pinus strobus* L.) (Brooks 2004), is perhaps as significant a threat to *T. canadensis* as HWA itself (Orwig et al. 2002). Pre-emptive "salvage" logging causes more abrupt ecological changes than the gradual decline of hemlock trees caused by HWA including greater amounts of regeneration by shade-intolerant species, higher soil pH, and higher nitrification rates (Kizlinski et al. 2002). Hemlock is typically replaced in this region by black birch (*Betula lenta* L.), *Q. rubra*, and red maple (*Acer rubrum* L.) (Orwig and Foster 1998). Little is known regarding how the loss of the hemlock-dominated forest type and homogenization of the overall diversity of forest types across the landscape will impact associated wildlife (Orwig et al. 2002).

The Relative Abundance of Red-backed Salamanders at the Harvard Forest

The research presented in Chapter 2 of this thesis was motivated by an earlier study I conducted at the Harvard Forest between Fall 2003 and Fall 2004, which found the relative abundance of *P. cinereus* to be significantly higher in hemlock-dominated stands in three of four seasons (Mathewson in review) (Figure 1). These findings were somewhat surprising, as prior to this study the relative abundance of *P. cinereus* had been found to be lower in conifer forests in the east, due to low soil pH (DeGraaf and Rudis 1992; Wyman and Jancola 1992).

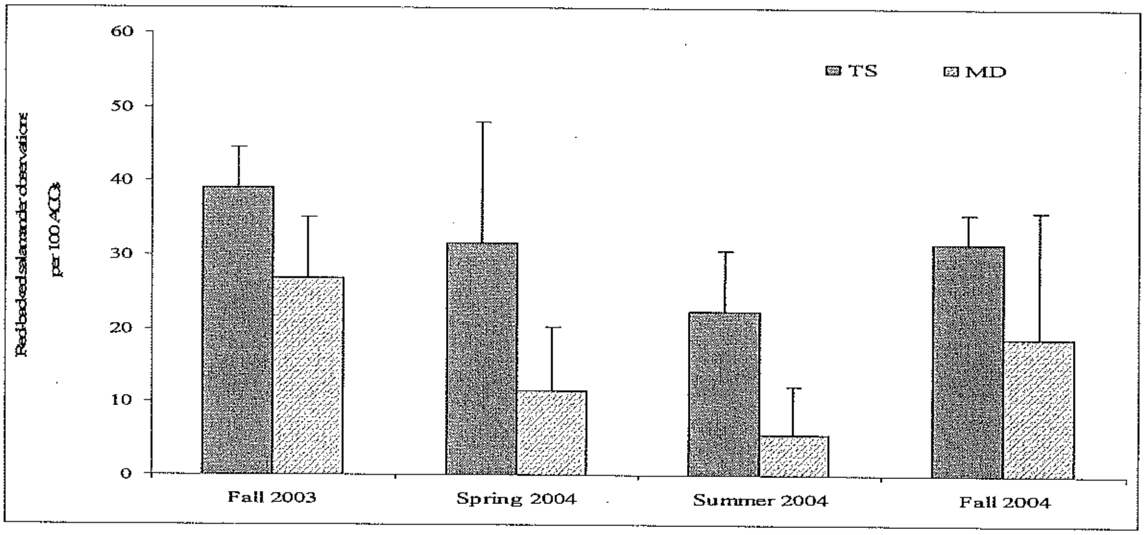

Figure 1. Eastern red-backed salamander (*Plethodon cinereus*) relative abundance in five eastern hemlock dominated stands (TS) and five mixed deciduous stands (MD) at Harvard Forest over four seasons. Error bar indicates one standard deviation.

My goal for the current study was to determine whether the higher relative abundance of *P. cinereus* in hemlock-dominated found at Harvard Forest extends to all of north-central Massachusetts. A cooler and moister microclimate, potentially higher volumes of CWD, and higher abundance of invertebrates suggest that, provided soil pH is not too low, hemlock-dominated forests provide high quality *P. cinereus* habitat. For this reason I hypothesized that the relative abundance and body condition of *P. cinereus* would be higher in hemlock-dominated forests than in mixed deciduous forests. This study also examines potential differences in the size class structure and factors influencing the relative abundance and body condition of *P. cinereus*. These questions are important given the ecological importance of *P. cinereus* and the threat of the loss of hemlock-dominated forests due to HWA.

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CHAPTER 2

Differences in Eastern Red-backed Salamander (*Plethodon cinereus*) Populations in Eastern Hemlock (*Tsuga canadensis*) Dominated and Mixed Deciduous Forests

Abstract

Throughout the twentieth century several dominant tree species suffered severe decline in the eastern United States due to exotic pests and pathogens, yet little is known of the effects these losses have on ecosystem processes or associated wildlife populations. Eastern hemlock (*Tsuga canadensis*), an important late-successional tree species, is currently threatened throughout its range by the hemlock woolly adelgid (*Adelges tsugae*; HWA), an invasive insect pest native to Japan. The unique structure and microenvironment of hemlock-dominated forests create critical landscape level heterogeneity, providing habitat for numerous bird and mammal species several of which are strongly associated with hemlock stands in the Northeast. The effects of hemlock loss on associated wildlife is largely unknown, but is of particular concern for terrestrial salamanders as they are sensitive to microclimatic conditions that are likely to change as hemlocks decline. In this study, populations of eastern red-backed salamanders (*Plethodon cinereus*), significant contributors to the overall vertebrate biomass in northeastern forests, are compared in hemlock-dominated and mixed deciduous forest. Artificial cover objects (ACO) were monitored in fifteen paired hemlock-dominated and mixed deciduous plots in north central Massachusetts. Size class distribution differed between forest types with a higher percentage of large *P. cinereus* found in hemlock-dominated forests. The best predictor of variation in the relative abundance of *P.*

cinereus was relative humidity and soil pH in hemlock-dominated forests and soil temperature in mixed deciduous forests. No statistically significant ($p < 0.05$) model could be generated to predict variation in the body condition of *P. cinereus* in hemlock-dominated forests. Percentage of white pine (*Pinus strobus*) and black birch (*Betula lenta*) were the most important predictors of body condition in mixed deciduous plots. Surprisingly, no difference was observed in the relative abundance or body condition of *P. cinereus* in the two forest types. This study suggests that *P. cinereus* populations in hemlock-dominated and mixed deciduous forests differ in subtle, but important ways.

Introduction

Throughout the twentieth century several dominant tree species, such as American beech (*Fagus grandifolia* Ehrh.), American chestnut (*Castanea dentata* (Marshall) Borkh.), and American elm (*Ulmus Americana* L.), suffered severe declines in the northeastern United States due to exotic pests and pathogens, yet little is known concerning the effects of these losses on ecosystem processes or associated wildlife populations (Orwig 2002). More recently, eastern hemlock (*Tsuga canadensis* (L.) Carr.), has suffered high levels of mortality across much of its range in eastern North America and it is expected that hemlock-dominated forests will be lost or greatly reduced across the region within the next few decades due to the hemlock woolly adelgid (*Adelges tsugae*; henceforth "HWA") (Orwig and Foster 1998; Ellison et al. 2005). Hemlock-dominated forests are structurally unique (Orwig and Foster 1998); hemlock is a shade-tolerant conifer that retains its foliage and lower branches, and forests dominated by this species are vertically complex with dense canopies that create a dark, cool, moist microenvironment with a depauperate understory (Rogers 1978; Benzinger 1994a). Hemlock needles are acidic and slow to decompose and soil pH and nitrogen cycling rates in hemlock-dominated forests are lower than in mixed deciduous forests (Benzinger 1994a; Jenkins et al. 1999). This distinct microenvironment provides habitat to at least ninety-six species of birds and forty-seven species of small mammals in the Northeast, several of which are regionally uncommon and strongly associated with hemlock (Yamasaki et al. 2000; Benzinger 1994b). Hemlock-dominated forests are also unique in that some ecologically important species, for example the brood parasite, brown-headed cowbird (*Molothrus ater* Boddaert) and ant species in the *Formica* genus are generally absent (Benzinger 1994b; Tingley et al. 2002; Ellison et al. 2005).

In temperate forests, terrestrial salamanders are ecologically important as both predators and prey (Burton and Likens 1975a; Welsh and Droege 2001). At Hubbard Brook Experimental Forest in Coos County, New Hampshire, terrestrial salamanders, 95% of which were eastern red-backed salamanders (*Plethodon cinereus* Green), were found to contribute significantly to the overall vertebrate biomass of forest ecosystems, accounting for as much biomass as small mammals and twice the biomass of breeding birds (Burton and Likens 1975a). Annually, *P. cinereus* is believed to consume a little more than the standing crop of soil fauna (Hairston 1987; Wyman 1998). As ectotherms with low metabolic demands, salamanders are extremely efficient at converting their prey into biomass, fixing 60% of digested material into new tissue (Burton and Likens 1975b). In addition, *P. cinereus* have very high protein content and are important as nutritious prey for many higher vertebrates (Petranka 1998). Finally, *P. cinereus* may play a role in regulating key ecosystem processes such as decomposition rates (Burton and Likens

1975b; Hairston 1987; Wyman 1998). Enclosures excluding salamanders had decomposition rates between 11% and 17% higher than enclosures containing salamanders (Wyman 1998).

HWA, an aphid-like insect, native to Japan, first appeared in Virginia in the 1950s (Souter et al. 1996). In Massachusetts, HWA is now found in 50% of eastern hemlock dominated forests, primarily in the southern and eastern portions of the state (Orwig et al. unpubl.). HWA feeds on the ray parenchyma cells of eastern hemlock needles (Young et al. 1995) on trees of all ages, killing them in 4-15 years (McClure 1990; Orwig pers. comm.). While overstory hemlock mortality is still generally very low in hemlock-dominated forests in Massachusetts (Orwig et al. unpublished data), in some forests in Connecticut where HWA was first found in 1985 it has reached 99% (Orwig and Foster 2000). There are no known effective native HWA predators in North America, and mortality is expected to increase throughout the Northeast in the coming decades (McClure 1995). In addition to the direct threat from HWA, hemlock trees are undergoing widespread pre-emptive salvage-logging in anticipation of HWA-induced hemlock decline (Orwig et al. 2002). In response to HWA or logging, eastern hemlock is replaced in this region by hardwood species such as black birch (*Betula lenta* L.), red oak (*Quercus rubra* L.), and red maple (*Acer rubrum* L.) (Orwig and Foster 1998).

Hemlock-dominated forests have several site characteristics which suggest that the relative abundance of *P. cinereus* would be higher in this forest type than others. As a lungless salamander, *P. cinereus* respires through its skin and must always remain moist to facilitate gas exchange (Feder 1983). Higher temperatures have been found to increase the food requirements of *P. cinereus*, while also causing a decrease in digestive efficiency (Bobka et al. 1981). The relative abundance of *P. cinereus* has been found to be higher in areas with cooler temperatures and higher soil moisture (Heatwole 1962; Grover 1998), both of which are strongly influenced by the percentage of hemlock in a stand. In hemlock-dominated forests, temperatures on the surface of the forest floor are lower in the spring and fall (Mathewson in review), and soils have a higher moisture content than mixed deciduous forests (Benzinger 1994a). In addition, soil fauna, including groups known to be important to the diet of *P. cinereus* such as Diptera and Coleoptera (Burton 1976) are more abundant in hemlock litter than in mixed deciduous litter (Hartman 1977).

Despite these favorable characteristics the relative abundance of *P. cinereus* may be lower in hemlock-dominated than mixed deciduous forest if the soil is too acidic. In Albany County, New York, amphibians were found to be less abundant in hemlock-dominated forests than in beech-dominated forests, presumably due to low soil pH (< 3.7) (Wyman and Hawksley-Lescault 1987; Frisbie and Wyman 1991; Wyman and Jancola 1992). In contrast, at Harvard Forest, where the average soil pH is higher than 3.7 in both hemlock-dominated stands (4.0) and oak-dominated stands (4.4), the relative abundance of *P. cinereus* was found to be higher in hemlock-dominated forests, (Mathewson in review).

The objectives of this study were: 1) to determine whether the relative abundance, body condition, and size class structure of *P. cinereus* populations differ in hemlock-dominated forests versus mixed deciduous forests in north-central Massachusetts. A difference in age-class structure in the two forest types may suggest a difference in survivorship, while differences in body condition are driven by differences in the energy expenditure required to obtain food resources and can lead to differences in reproductive success (Harder and Kirkpatrick 1996). 2) to evaluate how structure and microenvironment differ and determine which variables best predict the variation in relative abundance and body condition of *P. cinereus* in the two forest types. Results from earlier work as well as evidence that cooler, moister habitat and higher abundance of prey is found in hemlock-dominated forest led me to hypothesize that *P. cinereus* relative abundance and body condition would be higher in plots in this forest type.

Materials and Methods

Site selection

Fifteen paired, circular, 0.33 ha plots were distributed throughout north central Massachusetts (Figure 1) on land owned by the state of Massachusetts or Harvard University. This region is part of the transition hardwood-white pine forest (DeGraaf and Yamasaki 2001). The average annual precipitation of 130-140 cm, is relatively evenly distributed throughout the year. The mean January temperature is -5.8 °C and the mean July temperature is 22.3 °C (Hall et al. 2002). Granitic and metamorphic bedrock underlay glacial till, and associated acidic soils (Durand 2001; Hall et al. 2002). Plot elevation ranged from 212 m a.s.l to 560 m a.s.l., with slopes from flat to 17.8%.

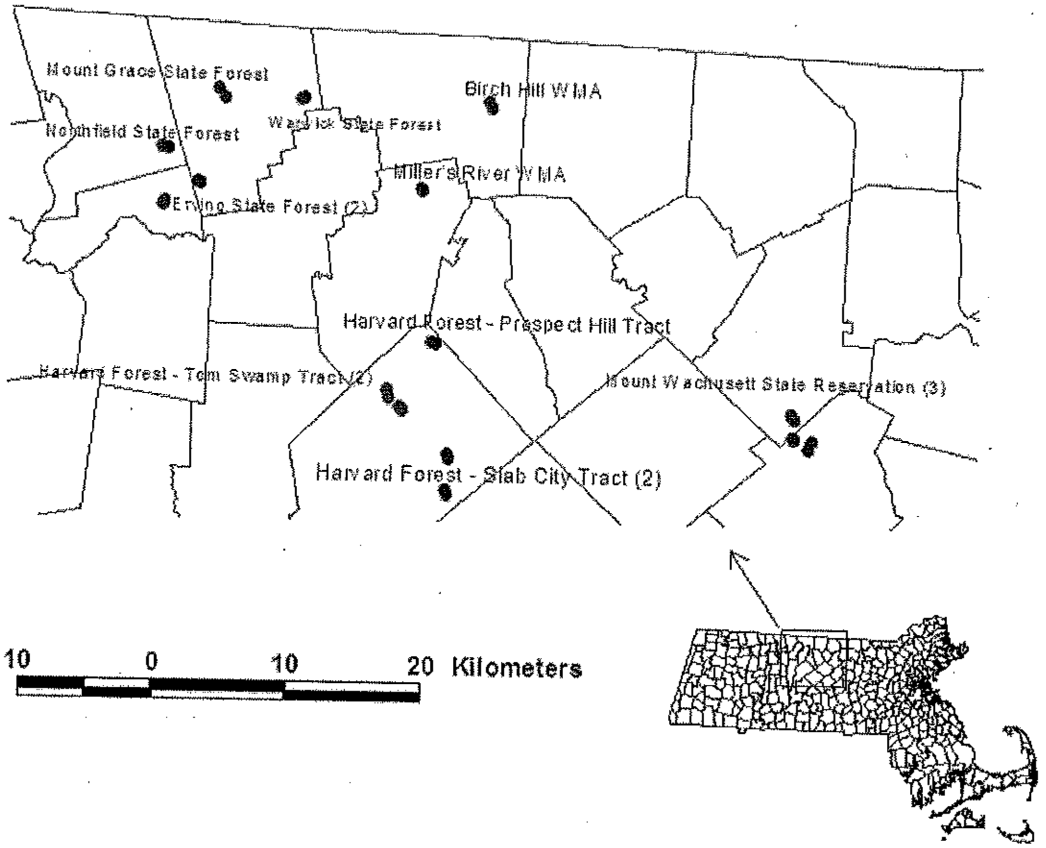


Figure 1. Location of fifteen paired hemlock-dominated and mixed deciduous plots in north central Massachusetts.

I used maps developed from aerial photography (Orwig et al. unpubl) to identify potential paired sites, less than 750 m apart, in which the basal area ($m^2 ha^{-1}$) of hemlock was greater than 50% in one and less than 25% in another. If field surveys confirmed that sites were likely to meet these criteria, a random center point, farther than 57.5 m from the edge of the stand, and compass heading were selected and perpendicular 50 m transects intersecting at the center point were established. ACO stations were then set up at the ends of each transect and at their intersection. At each ACO station a pair of green, rough-cut, untreated, 2-cm thick, 1 m x 0.25 m, eastern hemlock boards were installed

3m apart parallel to one another and the transect between May 11, 2005 and June 13, 2005.

Salamander Sampling

ACOs were used for several reasons. The installation and monitoring of standardized arrays of ACOs enables an equalized sampling effort which reduces the variability in probability of detection between plots (Fellers and Drost 1994; Droege 1997; Westereng and Quayle 1999). Additionally, ACOs can be sampled repeatedly with less direct and indirect impact on the species being sampled than sampling methods such as pitfall traps and natural cover searches (Fellers and Drost 1994; Droege 1997; Westereng and Quayle 1999). While ACOs have been used effectively in the past by previous studies (DeGraaf and Yamasaki 1992; Grant et al. 1992; Brooks 1999; Westereng and Quayle 1999; Monti et al. 2000; Brooks 2001; Houze and Chandler 2002; Marsh and Goicochea 2003), one concern regarding the use of ACOs is that differences in the amount, size, and/or decay class of natural cover objects at different sites may influence detection probabilities (Houze and Chandler 2002). This was addressed by measuring natural cover and examining its relationship with *P. cinereus* observation rates.

Each ACO was monitored every two to three weeks between June 13th, 2005 and November 4th, 2005 (n = 2380 ACO observations). This resulted in 8 salamander sampling dates per plot except at one site (Millers River Wildlife Management Area), which was sampled 7 times. Plots were sampled in order of installation for the first several rounds of monitoring. Subsequently, the order of sampling was selected randomly, although logistics required that sites close to one another be sampled on the same day. Paired hemlock-dominated and adjacent mixed deciduous plots at each site were always sampled on the same day. All amphibian and reptile species observed under ACOs were recorded. Snout-vent length (SVL) (+/- 1mm) was recorded for all amphibians, and weight (+/- 0.01g) and total length (TL) (+/- 1mm) were also measured for all *P. cinereus*. In addition, I attempted to identify the sex of all adult *P. cinereus* based on a qualitative analysis of snout shape: rounded – female; square – male (Gillette and Peterson 2001).

Habitat Sampling

At each ACO station a 7.5m radius fixed area sub-plot was established. Species and diameter-at-breast height (dbh) were recorded all trees greater than 5cm dbh, and for all dead trees greater than 1 m in height. From the center of each sub-plot three 7.5m transects oriented at 30°, 150°, and 270° were walked and the following were recorded for all coarse woody debris (CWD) (diameter > 2.5cm) (Harmon et al. 1986) encountered: diameter, species (if discernible), whether the object was touching the surface of the soil, and the decay class (1-5 scale defined by Liu et al. (in review)) (Wagner 1964). The organic soil was sampled in one location in each plot and the pH of a slurry of 2.0g of organic soil and 20ml of deionized water determined using an Orion 270 pH meter (Hendershot et al. 1993). Aspect and slope were recorded and canopy cover estimated using a spherical densiometer. In addition, during each ACO monitoring visit to a plot, soil temperature at 5cm, air temperature on the surface of the soil, and relative humidity on the surface of the soil was measured at one randomly selected ACO.

Statistical Analysis

Relative abundance data for *P. cinereus* followed a Poisson distribution and were square root transformed before all analyses. A body condition index value for each *P. cinereus* captured was calculated as the residual of the regression of the population's log-transformed body mass on the log-transformed total length (Harris and Ludwig 2004; Marsh and Beckman 2004). Three size classes were established based on snout-vent length (SVL): large (> 35mm SVL), intermediate (20-35 SVL), and small (<20 mm SVL) (Sayler 1966; Grover 1998). One-way ANOVA with site as a blocking variable was used to test for the effect of forest type on the relative abundance and the body condition of large, intermediate, and all *P. cinereus*. Shapiro-Wilk (1965) goodness-of-fit tests were conducted to verify that all distributions were normally distributed for all ANOVA tests. Chi-square analysis was used to test for a difference in distribution of the three size-classes, and for a difference in male/female ratios between forest types. To test whether habitat variables were significantly different in hemlock-dominated and mixed deciduous stands, one-way ANOVA was used with site as a blocking variable.

Aspect was converted to the transformed radiative aspect (TRASAP) using the following formula: $\mathrm{TRASAP} = (1 - \cos((\pi/180)(\mathrm{aspect} - 30))/2$ (Roberts and Cooper 1989). Higher values reflect drier aspects to the south-southwest (Roberts and Cooper 1989). For regression analyses, red oak (*Quercus rubra* L.), black oak (*Quercus velutina* Lam.), and white oak (*Quercus alba* L.) were combined into one group. Linear regression analyses were used to identify predictors of the relative abundance and body condition of *P. cinereus* in hemlock-dominated plots and mixed deciduous plots using the following variables: percentage eastern hemlock, percentage eastern white pine (*Pinus* *strobus* L.), percentage oak species, percentage *F. grandifolia*, percentage black birch (*Betula lenta* L.), percentage red maple (*Acer rubrum* L.), elevation, TRASAP, slope (%), canopy cover (%), overstory density (stems ha^{-1}), overstory basal area (m^2 ha^{-1}), volume of coarse woody debris in contact with the soil (m^3 ha^{-1}), average decay class of CWD, soil pH, soil temperature, air temperature, and relative humidity. Prior to running these analyses I ran multicollinearity tests for correlations between predictor variables. Variables which had a correlation coefficient > 0.70 were not included together. The same set of initial predictor variables was used to create models for both forest types. I looked at all models using adjusted r^2 and AIC as criteria for including predictor variables in the model. The residuals from all regression models were tested for goodness-of-fit using the Shapiro-Wilk (1965) test.

To address the concern that detection probabilities under ACOs vary based on the amount of natural cover available (Brooks 1996), I used Pearson's correlation tests to determine correlations between the relative abundance of *P. cinereus* and the following: number of pieces of coarse woody debris encountered during transect walks, number of pieces of coarse woody debris in contact with the soil encountered during transect walks, volume of coarse woody debris, and volume of coarse woody debris in contact with the soil. A negative correlation between any of these measurements and the relative abundance of *P. cinereus* would be a cause for concern as this would suggest that less habitat was resulting in higher estimates of relative abundance. The number of pieces of coarse woody debris in contact with the soil encountered during transect walks followed a Poisson distribution and these data were square root transformed. The volumes of coarse woody debris and coarse woody debris in contact with the soil were logarithmically transformed.

Results

Two hundred ninety-seven individuals of seven species of amphibians and reptiles were found under ACOs (Table 1). Of the 250 *P. cinereus* observed, 245 were successfully captured, weighed, measured, and released. In two of the fifteen paired plots, one of the plots did not meet the criteria that the percentage basal area of eastern hemlock be greater than 50% in hemlock-dominated plots and less than 25% in mixed-deciduous plots (Table 2). These pairs were excluded from ANOVA analyses of relative abundance and body condition and chi-square analyses of age class structure and sex ratio. In three paired plots no adults were found in at least one of the stands, and in four others no juveniles were found in at least one stand. These sites were removed from the appropriate analyses.

Table 1. Herpetofaunal observations under artificial cover objects (ACO) (n = 2380 ACO observations) in thirty plots in north-central Massachusetts (TS – hemlock-dominated plot (> 50% hemlock); MD – mixed deciduous plot (< 25% hemlock); Other - (25% > hemlock < 50%)).

Species	TS	MD	Other	Total
Eastern red-backed salamander (*Plethodon cinereus*)	123	109	18	250
Eastern red-spotted newt (*Notophthalmus v. viridescens*)	22	11	0	33
Wood frog (*Rana sylvatica*)	3	1	0	4
Two-lined salamander (*Eurycea bislineata*)	0	0	3	3
Spotted salamander (*Ambystoma maculatum*)	2	1	0	3
Northern redbelly snake (*Storeria o. occipitomaculata*)	0	2	0	2
Garter snake (*Thamnophis sirtalis*)	0	1	0	1

Table 2. Vegetative, physical, and climatic characteristics (measured at time of ACO monitoring) of fifteen paired plots in north-central Massachusetts. Italicized plots were not included in comparisons among forest types.

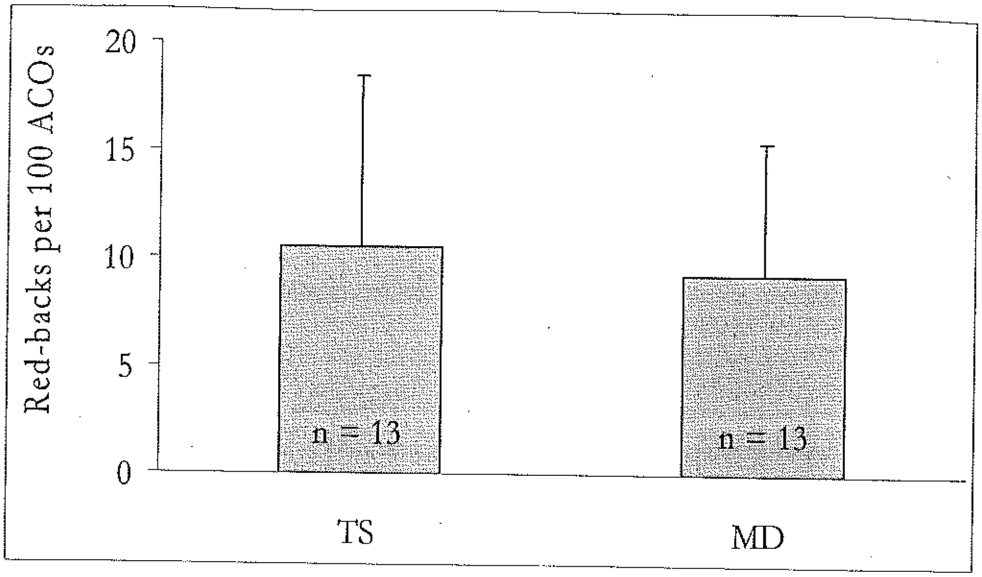
	ER2		WSF		SC1		*SC2*		TS1		NSF		*WA3*		MG	
	TS	MD	TS	MD	TS	MD	*TS*	*MD*	TS	MD	TS	MD	*TS*	*MD*	TS	MD
Relative basal area (%)																
Tsuga canadensis	56	22	79	19	73	0	*64*	*31*	51	11	64	12	*33*	*2*	66	21
Quercus spp.	0	12	8	16	5	38	*18*	*24*	19	55	6	48	*0*	*1*	0	8
Acer rubrum	6	31	4	14	7	32	*2*	*15*	2	14	14	15	*24*	*11*	8	15
Pinus strobus	5	0	0	0	0	10	*7*	*1*	8	16	11	1	*0*	*19*	6	16
Betula lenta	21	11	1	0	4	0	*4*	*3*	17	2	1	8	*15*	*4*	16	12
Fagus grandifolia	1	14	8	20	1	0	*5*	*12*	2	0	1	14	*0*	*1*	0	14
Physical Chars.																
Elevation (m)	212	240	210	222	270	259	*243*	*270*	240	273	264	288	*420*	*450*	270	300
Aspect	NW	W	N	E	E	E	*SW*	*NW*	NW	SW	E	SW	*NW*	*NW*	SW	E
Slope (%)	15.2	13.8	6	4	17.8	7.6	*12.6*	*17.4*	11.2	11.8	4	5.4	*7.6*	*12.8*	9.2	9.25
Canopy cover (%)	93	95	91	93	90	87	*91*	*93*	94	89	94	96	*92*	*91*	91	92
Overstory density (# ha^{-1})	1313	894	985	1109	1030	849	*883*	*1517*	702	1585	973	872	*713*	*905*	815	792
Overstory basal area (m^2 ha^{-1})	40.6	30.0	44.3	36.4	42.9	27.4	*55.5*	*39.5*	46.1	32.2	54.6	35.6	*43.9*	*34.6*	45.2	27.3
Vol. of CWD (m^3 ha^{-1})	24.8	111.3	21	26	61.7	30.1	*16.9*	*34.8*	24.0	17.9	7.6	35.4	*25.2*	*32.6*	43.5	29.8
Vol. of CWD touching soil (m^3 ha^{-1})	20.3	70.7	14.3	23.4	33.9	26.5	*16.3*	*33.2*	19.8	16.2	7.1	30.7	*20.9*	*24.3*	29.8	21.0
Avg. decay class of CWD	3.2	3.0	3.0	3.2	3.8	3.4	*3.1*	*3.6*	3.2	2.8	2.5	3.8	*3.2*	*3.7*	3.0	3.0
pH	3.8	4.1	3.7	4.1	3.8	4.2	*3.6*	*3.8*	3.8	3.6	3.6	3.5	*4.5*	*4.3*	3.7	3.8
Climate (at time of ACO monitoring)																
Avg. air temp	20.5	20.9	20.1	19.5	19.9	21.2	*20.5*	*20.1*	21.6	22.5	19.6	20.1	*19.8*	*19.9*	19.2	19.1
Avg. soil temp	16.5	16.4	16.2	15.8	16.6	16.8	*16.5*	*16.6*	17.2	17.9	15.5	16.3	*15.8*	*15.8*	15.9	15.8
Avg. relative humidity	75	74	83	85	84	82	*80*	*80*	81	79	82	81	*72*	*73*	81	84
Plethodon cinereus																
Abund. (per 100 ACOs)	22.5	16.3	11.3	23.8	26.3	6.3	*19.0*	*11.0*	21.3	5.0	10.0	13.8	*11.3*	*14.0*	6.3	11.3
Body condition	-0.01	-0.01	0.02	-0.05	0	0	*-0.09*	*-0.01*	0.02	0.10	0.02	-0.02	*0.03*	*-0.03*	-0.04	0.12

Table 2 (continued).

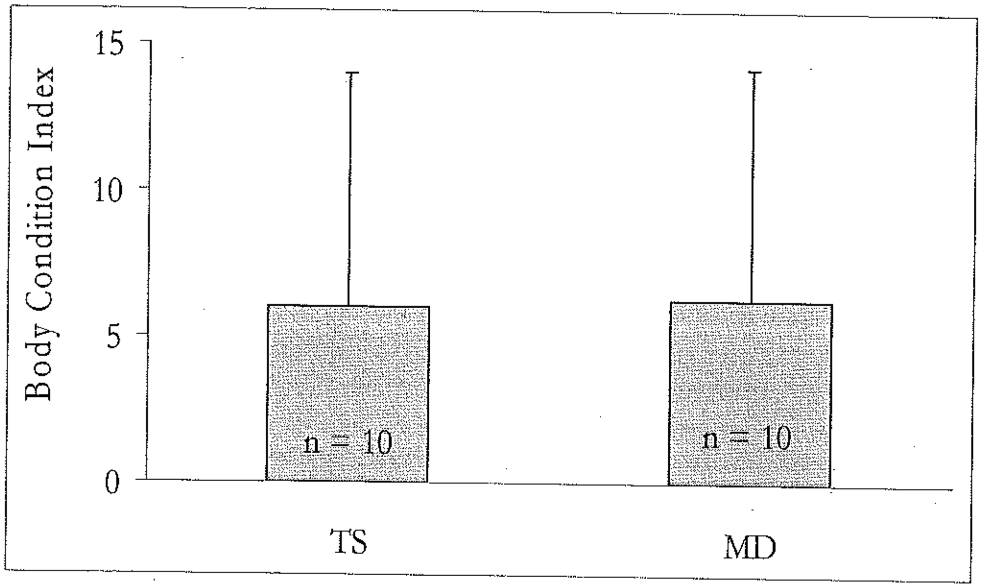
	ER1		PH		TS2		WA2		BH		WA1		MR	
	TS	MD	TS	MD	TS2	MD	TS	MD	TS	MD	TS	MD	TS	MD
Relative basal area (%)														
Tsuga canadensis	69	2	60	0	63	12	56	0	64	13	91	0	79	1
Quercus spp.	1	8	0	76	21	53	20	84	2	28	3	52	0	36
Acer rubrum	1	26	2	12	7	21	1	3	13	18	0	22	6	28
Pinus strobus	22	24	35	1	9	10	0	0	0	25	4	0	9	2
Betula lenta	7	26	3	1	0	0	22	0	2	1	2	18	1	0
Fagus grandifolia	0	1	0	6	0	0	0	12	6	0	0	5	4	0
Physical Chars.														
Elev(m)	240	246	360	375	237	249	520	560	279	285	470	440	255	270
Aspect	NE	NE	*	S	SW	E	W	SE	S	W	NW	W	W	W
Slope	7.4	8.8	*	7	9	9.4	15.6	17.4	5	5	10.6	5.6	15.5	14.8
Canopy cover	94	93	94	91	93	91	93	89	91	89	89	94	87	78
Overstory density (st ha^{-1})	1041	1114	668	1426	1188	838	555	826	1698	1132	838	815	792	1449
Overstory basal area (m^2 ha^{-1})	48.0	32.2	52.5	18.1	42.9	35.8	55.3	28.3	32.6	34.9	58.0	25.9	38.6	11.8
Vol. of CWD (m^3 ha^{-1})	16.0	24.8	29.0	6.5	15.4	34.4	87.6	20.0	23.9	35.5	38.3	19.1	27.9	13.7
Vol. of CWD touching soil (m^3 ha^{-1})	13.8	20.3	12.9	4.9	15.1	23.0	69.1	16.5	19.0	31.6	35.2	10.66	18.4	13.4
Avg. decay class of CWD	2.8	2.8	4.1	3.7	3.5	3.7	3.3	3.2	3.4	3.4	3.6	2.9	3.1	3.0
pH	3.7	4.0	3.6	3.6	3.6	4.4	4.0	4.1	3.6	3.8	3.8	3.9	3.7	3.9
Climate (at time of ACO monitoring)														
Avg. air temp	19.7	20.9	20.1	21.9	21.6	21.7	20.1	19.8	21.2	20.9	18.8	19.0	21.2	24.2
Avg. soil temp	16.3	16.5	16.2	17.4	16.8	16.5	16.1	17.2	16.6	17.0	15.8	16.6	16.3	19.1
Avg. relative humidity	77	81	83	77	84	83	69	70	76	80	67	62	78	74
Plethodon cinereus														
Abund. (per 100 ACOs)	8.8	7.5	6.3	10.0	7.5	8.8	10.0	1.3	1.3	10.0	1.3	6.3	4.3	1.4
Average body condition	0.09	-0.06	0.14	-0.01	-0.02	-0.03	0.05	-0.04	0.10	0.12	0.19	-0.19	-0.09	0.01

There was no significant difference in the average relative abundance of *P. cinereus* in hemlock-dominated and mixed deciduous plots (one-way ANOVA: F = 1.30; df = 25; $p = 0.329$; Figure 2a). In addition, the average body condition of *P. cinereus* was not significantly different in two forest types for individuals in the large size class (one-way ANOVA: F = 0.91; df = 19; $p = 0.555$; Figure 2b) intermediate size class (one-way ANOVA: F = 0.54; df = 17; $p = 0.800$; Figure 2c), or all size classes combined (one-way ANOVA: F = 1.34; df = 25; $p = 0.269$). Size-class distributions differed significantly among the two forest types (Pearson's $\chi^2 = 8.648$; df = 2; $p < 0.05$) (Table 3), with hemlock-dominated forests having a larger percentage of large individuals. No difference was found in the distribution of adult males and females in the two forest types (Pearson's $\chi^2 = 0.65$; df = 102; $p = 0.789$).

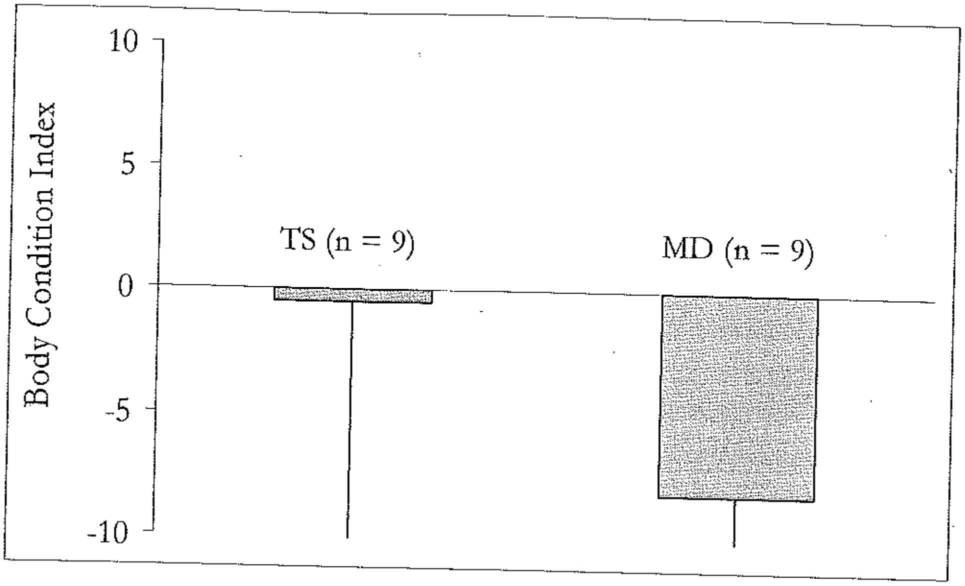
Hemlock-dominated plots occurred at lower elevations than mixed deciduous plots (one-way ANOVA; F = 6.98; df = 25; $p < 0.05$) and had higher basal area (one-way ANOVA; F = 35.17; df = 25; $p < 0.001$) (Table 4). Soil pH (one-way ANOVA; F = 6.83; df = 25; $p < 0.05$), soil temperature at 5cm (one-way ANOVA; F = 5.97; df = 25; $p < 0.05$), and forest floor air temperature (one-way ANOVA; F = 4.86; df = 23; $p < 0.05$) were lower in hemlock-dominated plots. Overstory density, snag density, TRASAP, canopy cover, volume of CWD, average decay class of coarse woody debris, and relative humidity did not differ among forest types.



A. Comparison of the relative abundance of *P. cinereus* in two forest types.



B. Comparison of the body condition of *P. cinereus* in the large size class (SVL > 35mm) in two forest types.



C. Comparison of body condition of *P. cinereus* in the intermediate size class (20mm ≤ SVL ≤ 35mm) in two forest types.

Figure 2. Comparisons of the relative abundance and adult and juvenile body condition of *P. cinereus* in two forest types (TS: (> 50% eastern hemlock); MD:(< 25 % eastern hemlock) in north- central Massachusetts. Error bars represent one standard deviation from the mean.

Table 3. Size-class distribution of *P. cinereus* in eastern hemlock-dominated and mixed deciduous forests in north-central Massachusetts (Pearson's $\chi^2 = 8.648$; df = 2; $p < 0.05$). Size classes were determined based on snout-vent-length (SVL) (Large: SVL > 35mm; Intermediate: 20mm ≤ SVL ≤ 35mm; Small: < 20 mm).

Forest type	Large	Intermediate	Small
Hemlock-dominated	87	37	2
Mixed deciduous	63	38	9
All	150	75	11

Table 4. Comparison of habitat variables in eastern hemlock dominated plots and mixed deciduous plots throughout north central Massachusetts. The numbers in parentheses represent one standard deviation.

Variable	TS (n=13)	MD (n=13)
Relative abundance of TSCA**	67 (11)	9 (9)
Elev(m)*	294 (97)	308 (96)
TRASAP	0.514 (0.372)	0.543 (0.320)
Slope	11 (4)	9 (4)
Canopy cover	92 (2)	91 (5)
Overstory density (st ha^{-1})	969 (305)	1054 (276)
Overstory basal area (m^2 ha^{-1})*	46.3 (7.3)	28.9 (7.2)
Vol. of CWD (m^3 ha^{-1})	34.2 (15.8)	30.4 (15.8)
Avg. decay class of CWD	3.3 (0.4)	3.2 (0.3)
pH*	3.7 (0.1)	3.9 (0.3)
Air temp at ACO monitoring*	20.3 (0.9)	20.9 (1.5)
Soil temp at ACO monitoring*	16.3 (0.5)	16.9 (0.9)
Relative humidity at ACO monitoring	78 (5)	78 (6)

* indicates $p < 0.05$

** indicates $p < 0.001$

Due to multicollinearity the following variables were removed prior to multiple regression analyses: basal area, overstory density, elevation, volume of CWD, TRASAP, air temperature, and canopy cover. The following models predicted the most variation in the relative abundance of *P. cinereus* in hemlock-dominated plots: -41.37 + (0.21 * relative humidity) + (7.49 * soil pH) ($r^2 = 0.49$; $p < 0.05$), and in mixed deciduous plots: 13.75 + (0.67 * soil temp) ($r^2 = 0.54$; $p < 0.01$). No statistically significant model (at $p < 0.05$) could be generated to predict variation in body condition in hemlock-dominated plots. In mixed deciduous plots the following model best predicted variation in body condition of *P. cinereus*: -2.53 + (0.54 * percent white pine) + (0.51 * percent black birch) ($r^2 = 0.51$; $p = 0.0195$).

No correlation was found between the relative abundance of *P. cinereus* and number of pieces of CWD encountered during transect walks (Pearson's correlation test; r = 0.139; *p* = 0.498), number of pieces of CWD in contact with the soil encountered during transect walks (Pearson's correlation test; r = 0.114; *p* = 0.578), volume of CWD (Pearson's correlation test; r = 0.248; *p* = 0.221), volume of CWD in contact with the soil (Pearson's correlation test; r = 0.192; *p* = 0.347), or average decay class of CWD (Pearson's correlation test; r = 0.0566; *p* = 0.785). In addition, no correlation was found between the body condition of *P. cinereus* and the number of pieces of CWD encountered during transect walks (Pearson's correlation test; r = 0.057; *p* = 0.783), number of pieces of CWD in contact with the soil encountered during transect walks (Pearson's correlation test; r = 0.062; *p* = 0.764) volume of CWD (Pearson's correlation test; r = 0.134; *p* = 0.514), volume of CWD in contact with the soil (Pearson's correlation test; r = 0.049; *p* = 0.812), or average decay class of CWD (Pearson's correlation test; r = 0.223; *p* = 0.273).

Discussion

The sensitivity of terrestrial salamanders to environmental characteristics (e.g. soil moisture, soil temperature, and soil pH) that are strongly influenced by stand composition and structure suggests that salamander populations may be strongly affected by a conversion of hemlock-dominated forest to mixed deciduous forest as a result of HWA or salvage logging. I expected that the relative abundance and body condition of *P. cinereus* would be greater in hemlock-dominated forests versus mixed deciduous forests. Surprisingly, neither the relative abundance nor body condition of *P. cinereus* differed between the two forest types. However, *P. cinereus* populations in hemlock-dominated forest do appear to differ from those in mixed deciduous forest in north-central Massachusetts in subtle, but important ways. For one, hemlock-dominated forests appear to have a higher percentage of large *P. cinereus*. In addition, the factors that are most important in predicting variation in the relative abundance of *P. cinereus* differ in the two forest types. The absence of a negative correlation between CWD and the relative abundance and body condition of *P. cinereus* under ACOs suggests that there is no evidence that differences in natural cover in the plots caused bias in these estimates.

The higher percentage of large *P. cinereus* suggests a higher percentage of adults in hemlock-dominated plots (Sayler 1966; Grover 1998). One reason for this may be that predation rates are higher in mixed deciduous plots, making individuals less likely to survive to adulthood. Cooler temperatures and less sunlight reaching the forest floor may cause a lower abundance of important reptilian predators in hemlock-dominated forests such as garter snakes (*Thamnophis sirtalis*) (Arnold 1982) and ring neck snakes (*Diadophis punctatus*) (Uhler 1939). In addition, over wintering mortality rates have been found to be high in *P. cinereus* in northern populations, ranging from 50% to 100% (Taub 1961), and a higher percentage of adult *P. cinereus* in hemlock-dominated forest may be due to milder winter temperatures than in mixed deciduous forest.

Differences in soil temperature and soil pH may explain why the factors most important in predicting the relative abundance of *P. cinereus* were different in the two forest types. Soil temperatures in hemlock-dominated forests are sufficiently cool so as to make relative humidity and soil pH more important predictors of variation in the relative abundance of *P. cinereus*. In contrast in mixed deciduous forests, soil temperatures are somewhat higher and more variable, and thus this environmental variable becomes the most important predictor of variation in the relative abundance of *P. cinereus* in this forest type. The negative relationship between soil pH and the relative abundance of *P. cinereus* in hemlock-dominated forests is consistent with other studies that have documented a reduction in the relative abundance of *P. cinereus* at a pH of 3.7 or lower (Frisbie and Wyman 1991). Heatwole (1962) also found different environmental factors influenced the relative abundance of *P. cinereus* in different forest types. In his study *P. cinereus* distribution was limited by temperature in oak-pine-aspen forest, and by moisture in beech-maple-hemlock forest.

In mixed deciduous forests vegetation composition appears to have a greater effect on the body condition of *P. cinereus* than environmental factors. This is the first time overstory tree species composition has been found to be an important predictor of the body condition of *P. cinereus*. It is not clear whether the positive relationship between the body condition of *P. cinereus* and the percentage of white pine and black birch in mixed deciduous forests is caused directly by these overstory tree species or is an indirect result of other factors. For example, a high percentage of white pine in a plot may suggest that the plot is more likely to have been cleared in the past for agriculture including pasturing (Motzkin et al. 1999). Consequently soils in these plots may have lower C:N ratios due to past nitrogen additions (Compton and Boone 2004), which could result in more abundant or nutritious prey. However, *a posteriori* analysis revealed no difference in the percentage of white pine in plots that were open rather than wooded in 1830 (one-way ANOVA; df = 25; F = 1.67; p = 0.208). In addition, further *a posteriori* analysis revealed no difference in adult body condition in plots that were open versus forested in 1830 (one-way ANOVA; df = 25; F = 0.31; p = 0.580). The body condition of *P. cinereus* may be higher in plots with higher percentages of eastern white pine and black birch because the CWD of these species may provide higher quality habitat for *P. cinereus,* although further study would be required to determine the causal mechanisms. For example, white pine and black birch CWD may have important structural differences which provide more cool, moist microhabitat than is found in CWD of other tree species. It also may be possible that invertebrates on which *P. cinereus* prey are more abundant, or that deleterious fungi are less abundant, in the CWD of these species.

One potential explanation for the lack of a difference in the relative abundance and body condition of *P. cinereus* in the two forest types may be similarities in volume of CWD (Grover 1998). The lack of a correlation between CWD and the relative abundance and body condition of *P. cinereus* in this study may result from the sampling having occurred on sites with little variation in CWD. Estimates of CWD in old-growth hemlock-dominated forests in western Massachusetts are 2-6 times greater than those from this study (D'Amato unpublished data). Experimental studies have found that increases in cover object density result in increases in the relative abundance and body condition of *P. cinereus* (Grover 1998), and one of the reasons for the higher relative abundance of plethodontid salamander species in old growth forests in western North America is believed to be greater volumes of CWD (Welsh and Lind 1988; Dupuis et al. 1995). Similarities in canopy cover and TRASAP may suggest similar levels of soil moisture in the two forest types, which may also partially explain similarities in the relative abundance and body condition of *P. cinereus* (Heatwole 1962; Grover 1998). Finally, the ways in which the two forest types differ may have confounding impacts on the relative abundance and body condition of *P. cinereus*. That is, in some plots in hemlock-dominated forest the relative abundance and body condition of *P. cinereus* may be higher due to lower soil temperatures (Heatwole 1962; Jaeger 1980), but in others abundance and body condition may be lower due to low soil pH (Wyman 1988b; Wyman and Hawksley-Lescault; Wyman and Jancola 1992).

Baseline data presented here will enable future studies to detect potential changes in *P. cinereus* populations in north-central Massachusetts. Terrestrial salamanders are excellent indicators of overall forest health given their abundance (Burton and Likens 1975a; Hairston 1987), functional position in the middle of the food web (Wyman 1998; Rooney et al. 2000), sensitivity to anthropogenic and natural disturbances (Pough et al. 1987; Harpole and Haas 1999), and low annual population variation when compared to other forest organisms (Welsh and Droege 2001). Amphibian populations throughout the world are suffering widespread declines which are caused both directly (e.g. over exploitation, loss of habitat) and indirectly (e.g. climate change, emission of atmospheric pollutants) by human activity (Stuart et al. 2004; Bank et al. 2006). Results from this study suggest that *P. cinereus* populations are vulnerable to two potential changes brought on by human activity - soil warming caused by global climate change (Melillo et al. 2004) and decreases in soil pH due to nitrogen and sulfur deposition (Aber et al. 2004).

Conclusions

The loss of hemlock-dominated forests from north-central Massachusetts will likely cause subtle, but important changes in *P. cinereus* populations. The size-class distribution of *P. cinereus* populations in hemlock-dominated forests that shift to mixed deciduous forest will likely result in a lower percentage of large individuals. In addition, soil temperatures will likely have a larger impact on the relative abundance of *P. cinereus*. Interestingly, overall relative abundance and body condition of *P. cinereus* in the two forest types in this region do not differ, suggesting that in these ways *P. cinereus* populations may not change substantially as hemlock-dominated forests are converted to mixed deciduous forest. This study also provides evidence of a relationship between the body condition of *P. cinereus* and vegetation composition, specifically that in mixed deciduous forests the relative abundance of white pine and black birch appears to have a positive effect on the body condition of *P. cinereus*. Perhaps the most important contributions made by this study is the baseline data presented here which will allow future studies to assess changes in *P. cinereus* populations, an ecologically important organism and an excellent indicator of overall forest health.

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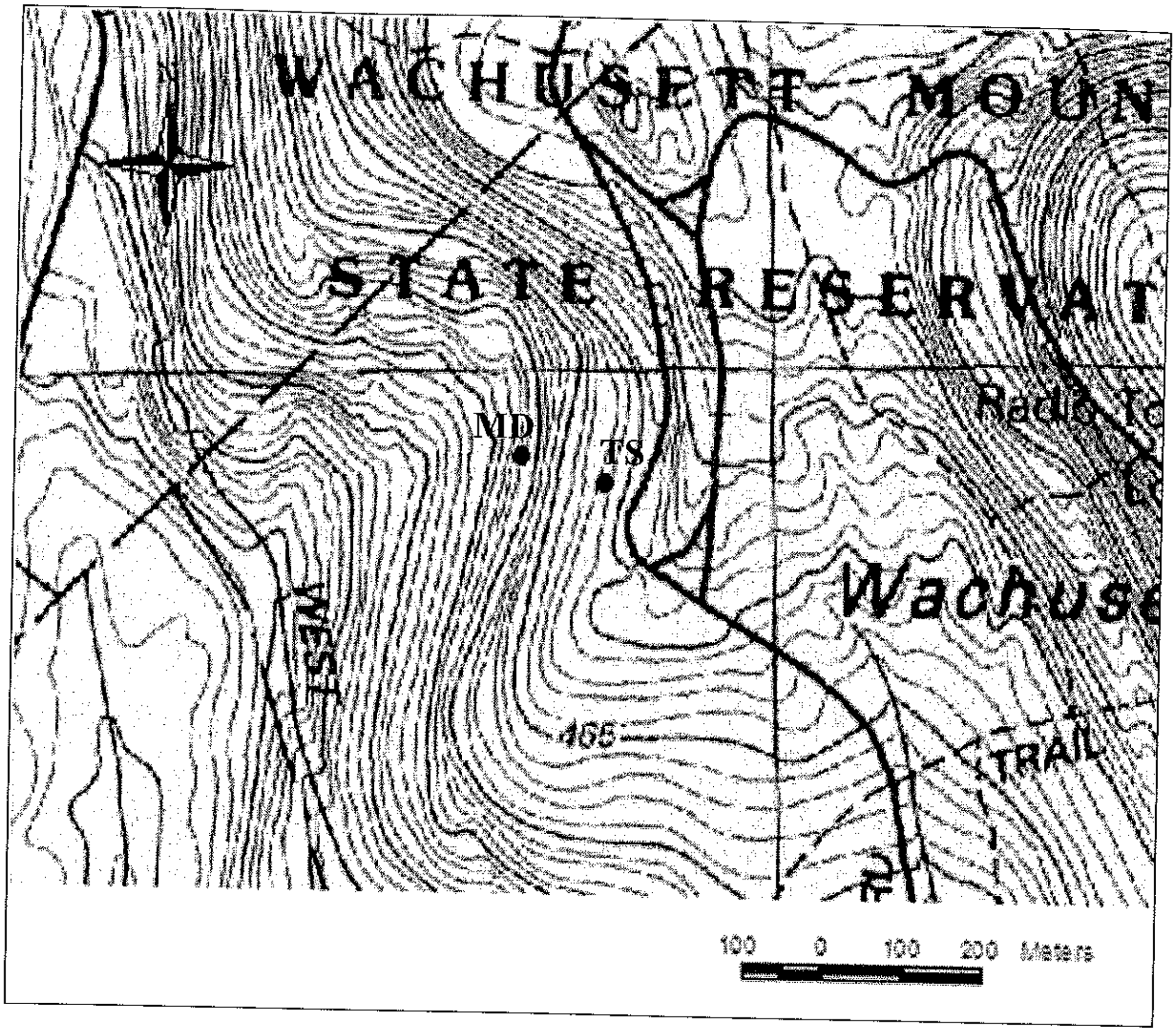
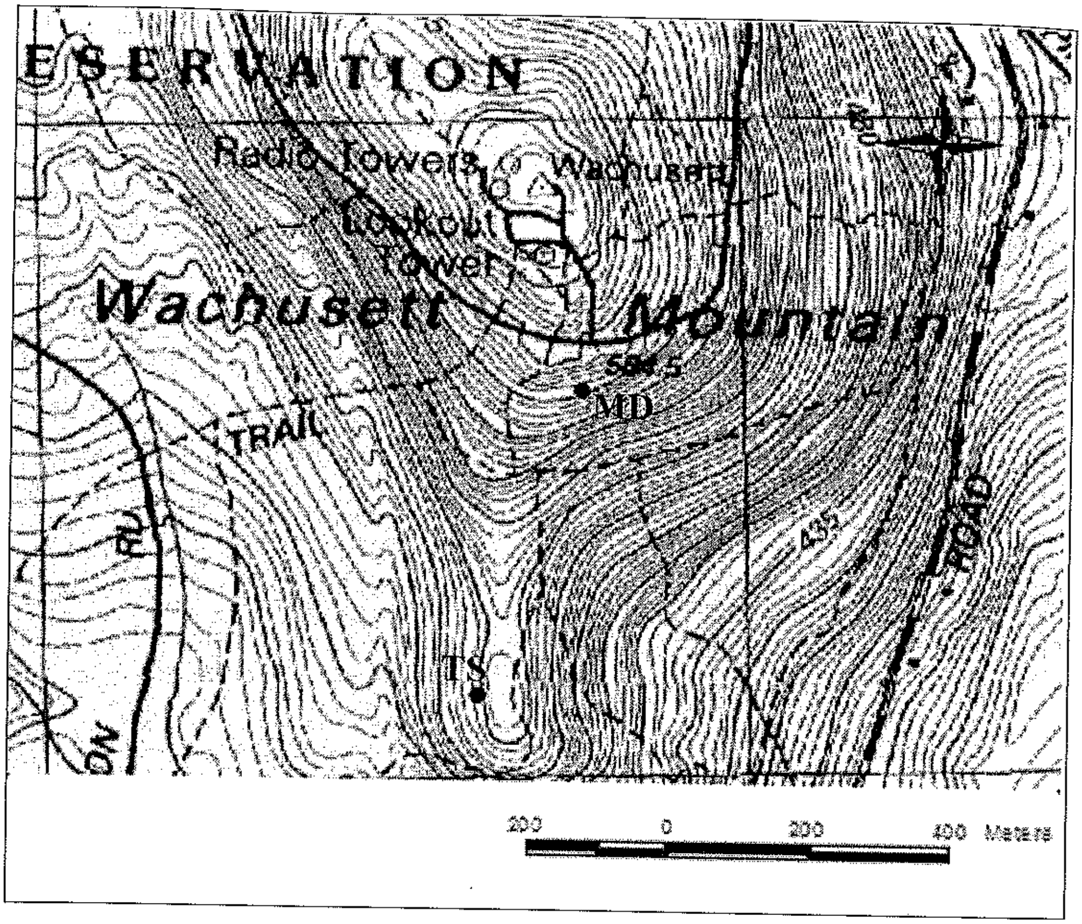
Appendix 1. Coordinates of center points of all study plots (Datum NAD 1983).

Site	Forest type	Lat	Long
Wachusett Mountain State Reservation 1 (WA1)	TS	N 42°29,275'	W 71°53.891'
	MD	N 42°29.315'	W 71°54.003'
Wachusett Mountain State Reservation 2 (WA2)	TS	N 42°28.946'	W 71°53.302'
	MD	N 42°29.179'	W 71°53.130'
Wachusett Mountain State Reservation 3 (WA3)	TS	N 42°30.110'	W 71°54.088'
	MD	N 42°29.984'	W 71°53.927'
Millers River Wildlife Management Area (MR)	TS	N 42°37.638'	W 72°11.624'
	MD	N 42°37.624'	W 72°11.561'
Birch Hill Wildlife Management Area (BH)	TS	N 42°40.744'	W 72°08.492'
	MD	N 42°40.556'	W 72°08.325'
Erving State Forest 1 (ER1)	TS	N 42°37.687'	W 72°21.965'
	MD	N 42°37.734'	W 72°22.121'
Erving State Forest 2 (ER2)	TS	N 42°37.042'	W 72°23.606'
	MD	N 42°36.923'	W 72°23.664'
Warwick State Forest (WSF)	TS	N 42°40.811'	W 72°17.155'
	MD	N 42°40.735'	W 72°17.259'
Northfield State Forest (NSF)	TS	N 42°38.917'	W 72°23.756'
	MD	N 42°38.899'	W 72°23.519'
Mount Grace State Forest (MG)	TS	N 42°40.741'	W 72°20.913'
	MD	N 42°41.031'	W 72°21.176'
Harvard Forest - Slab City 1 (SC1)	TS	N 42°28.491'	W 72°10.165'
	MD	N 42°28.320'	W 72°10.090'
Harvard Forest - Tom Swamp 1 (TS1)	TS	N 42°30.081'	W 72°12.387'
	MD	N 42°29.978'	W 72°12.265'
Harvard Forest - Prospect Hill (PH)	TS	N 42°32.310'	W 72°10.720'
	MD	N 42°32.343'	W 72°10.968'
Harvard Forest - Tom Swamp 2 (TS2)	TS	N 42°30.421'	W 72°12.891'
	MD	N 42°30.702'	W 72°13.000'
Harvard Forest - Slab City 2 (SC2)	TS	N 42°27.222'	W 72°10.155'
	MD	N 42°27.122'	W 72°10.087'

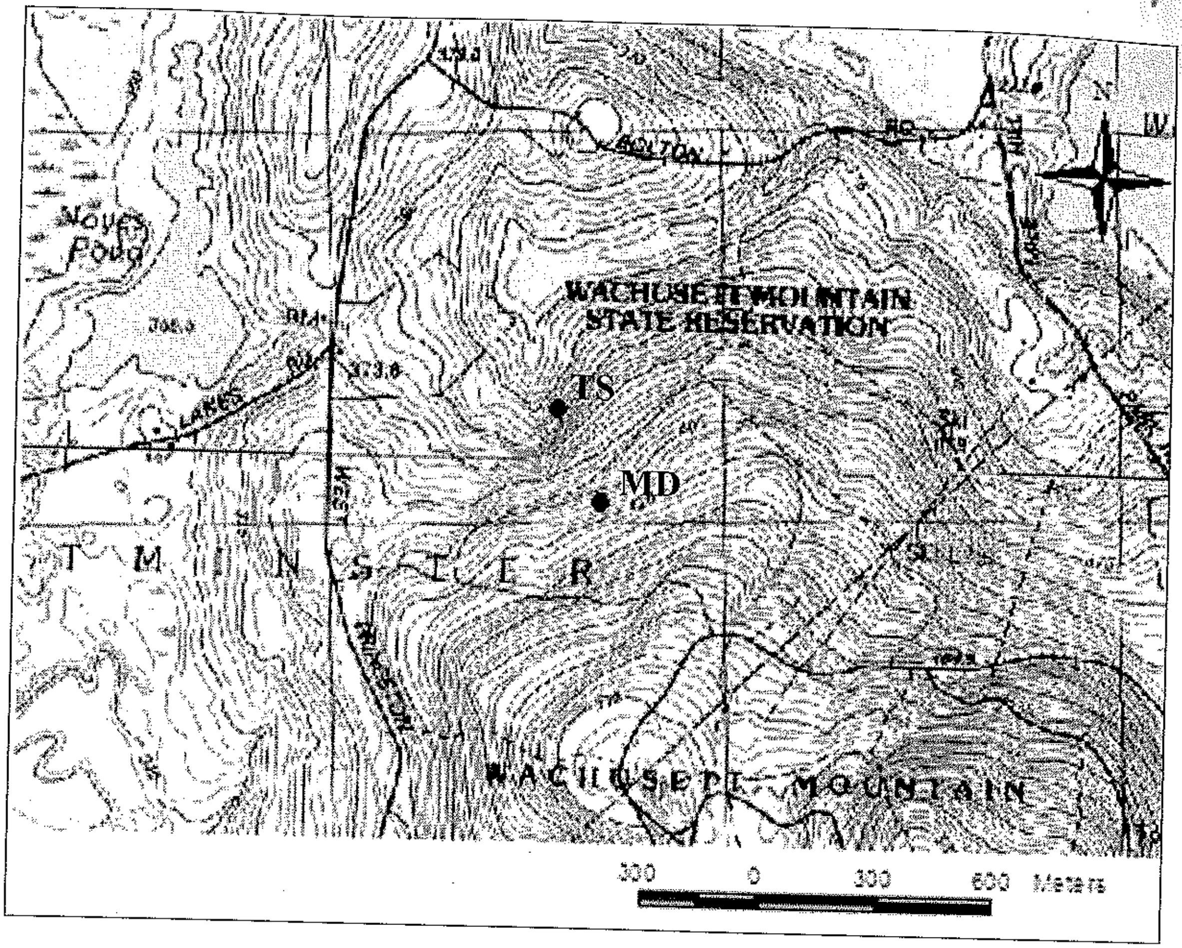
Appendix 2. Maps of all study plots.
(TS = location of hemlock-dominated plot; MD = location of mixed deciduous plots).



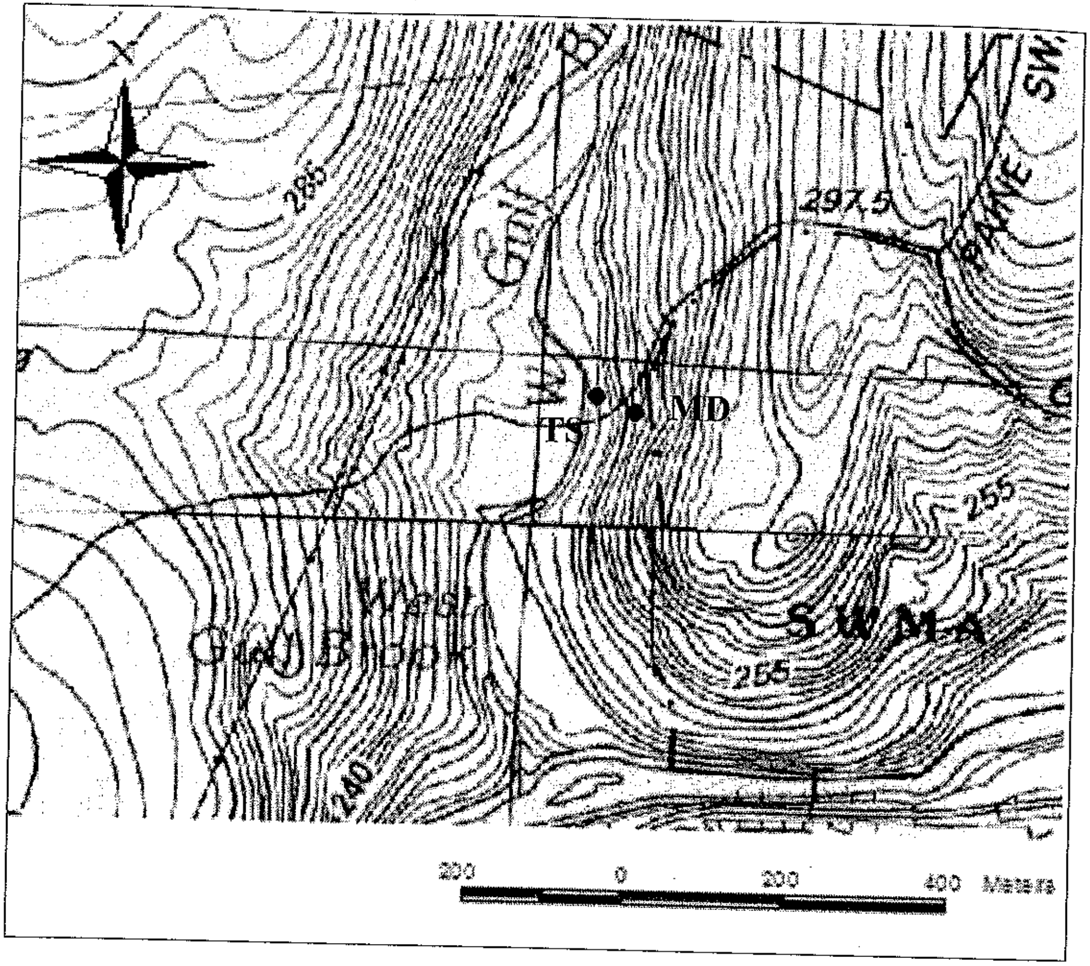
Map 1. Mount Wachusett State Reservation - Site 1 (WA1).



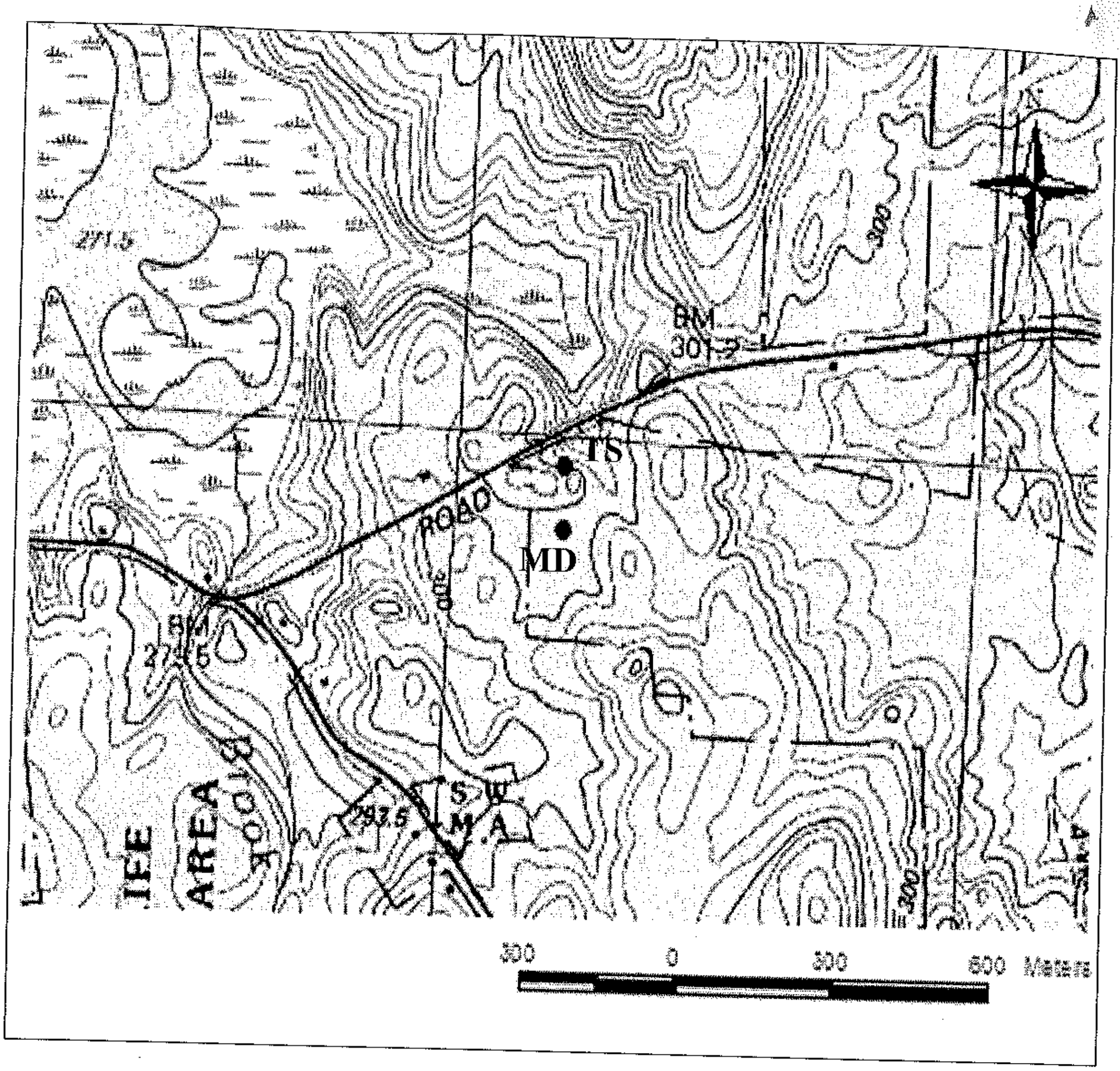
Map 2. Mount Wachusett State Reservation - Site 2 (WA2).



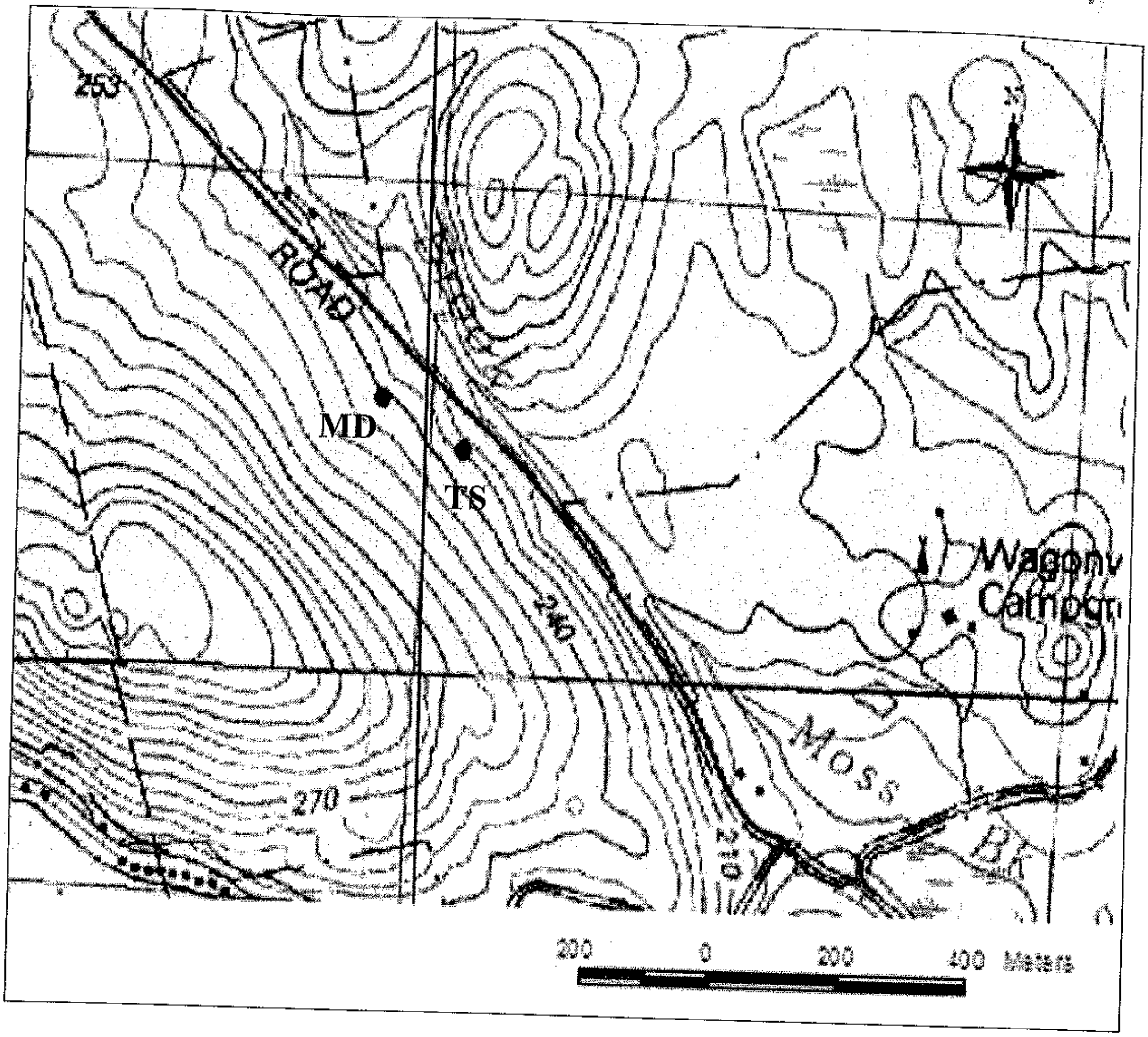
Map 3. Mount Wachusett State Reservation - Site 3 (WA3).



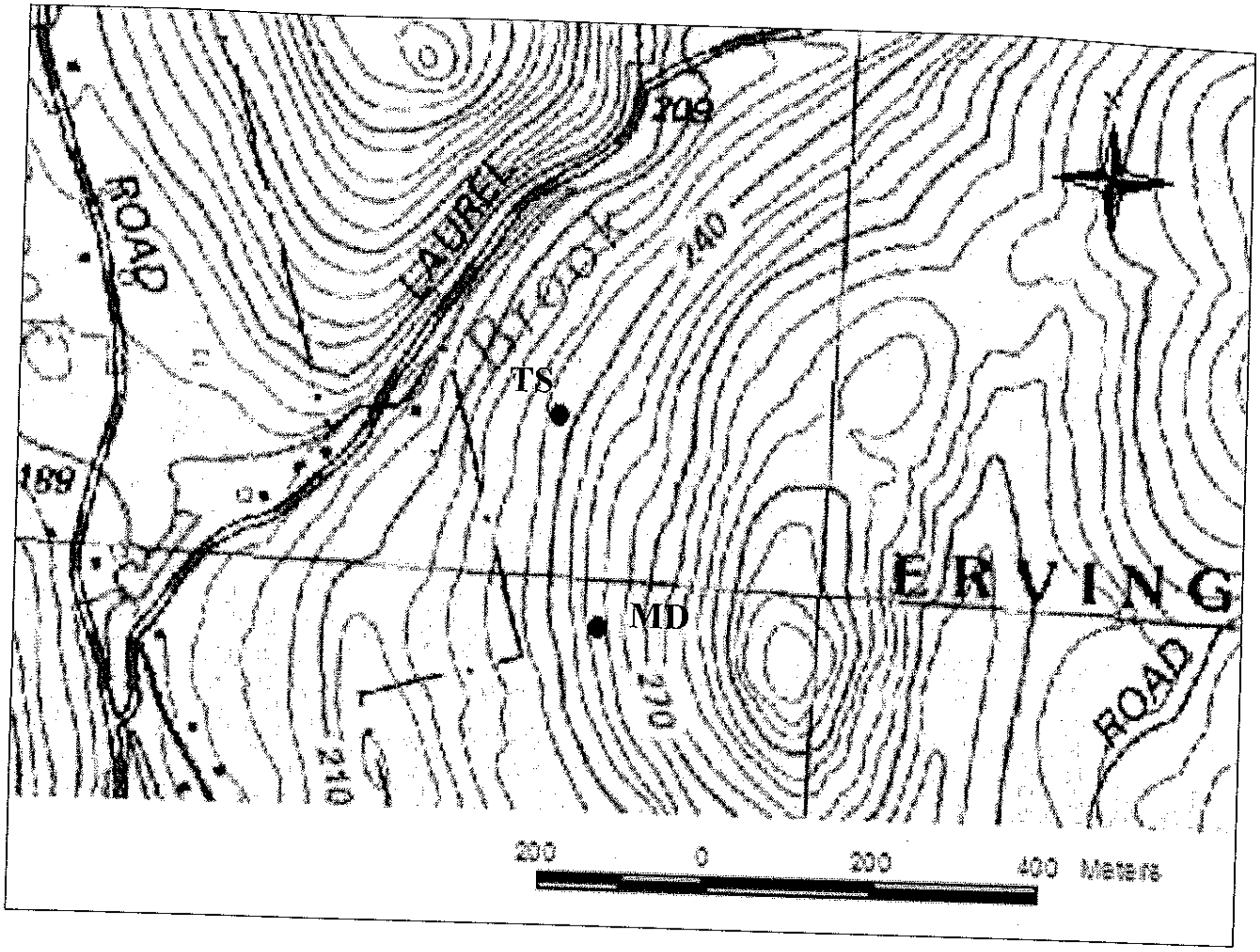
Map 4. Millers River Wildlife Management Area (MR).



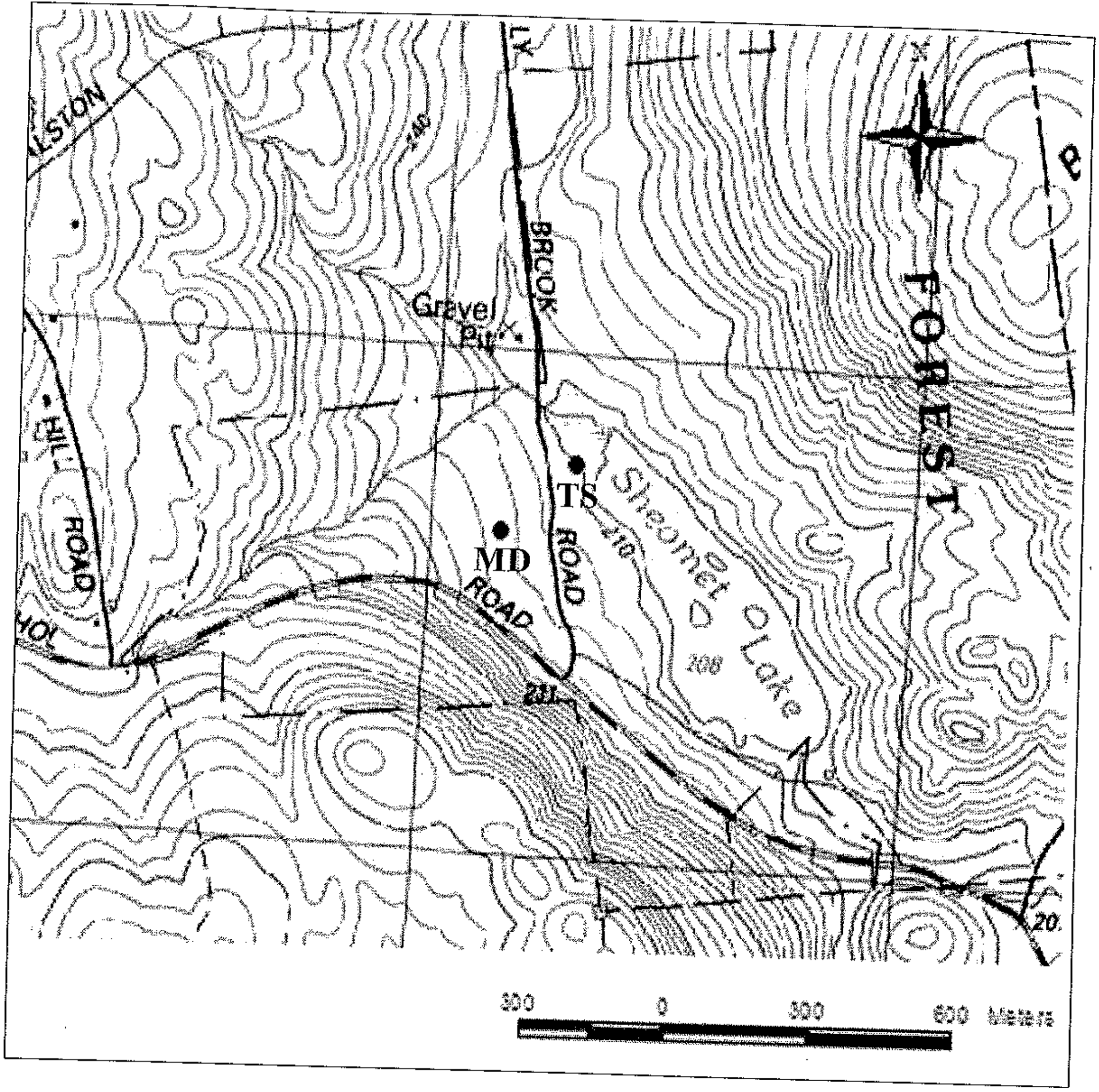
Map 5. Birch Hill Wildlife Management Area (BH).



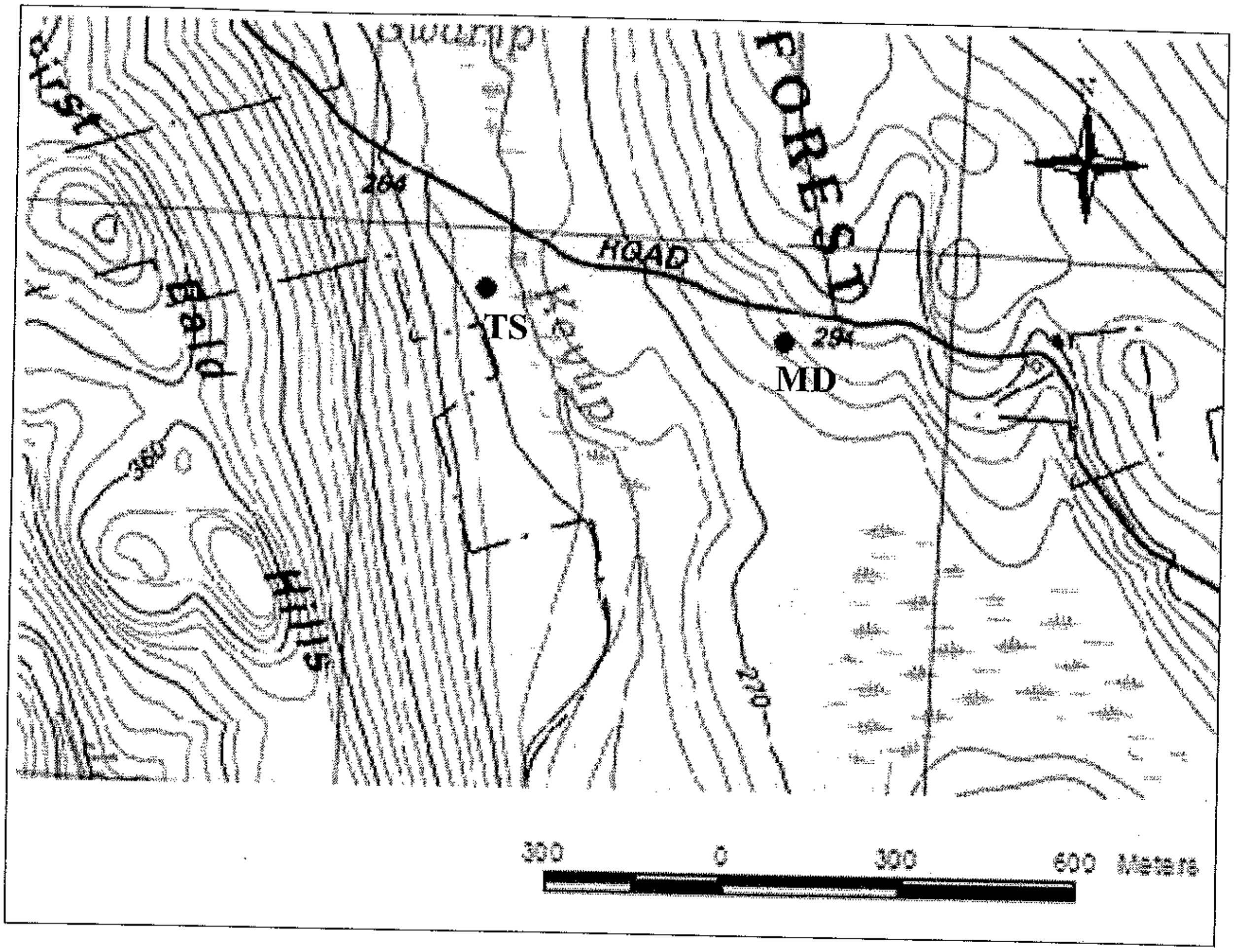
Map 6. Erving State Forest (ER1).



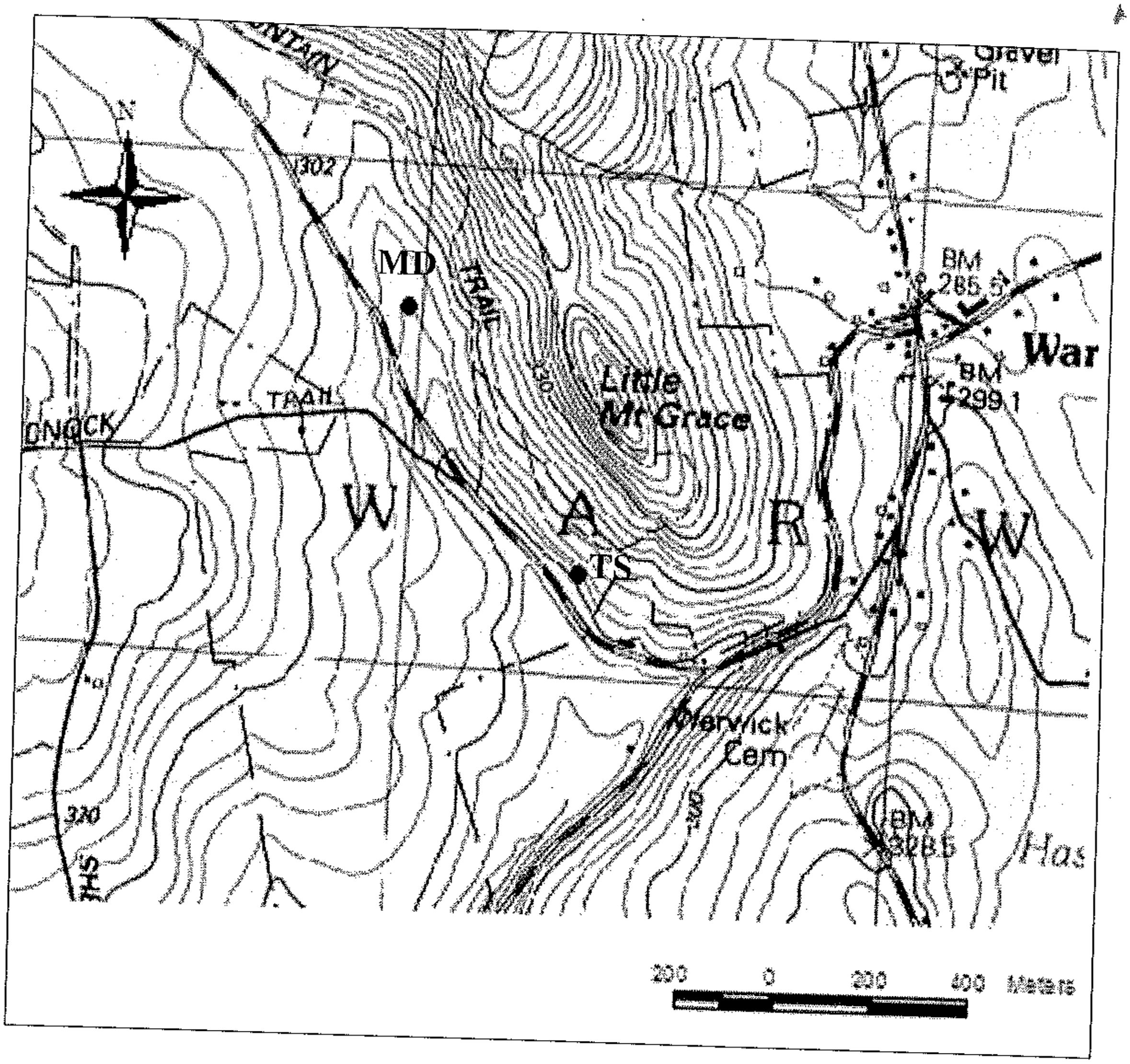
Map 7. Erving State Forest (ER2).



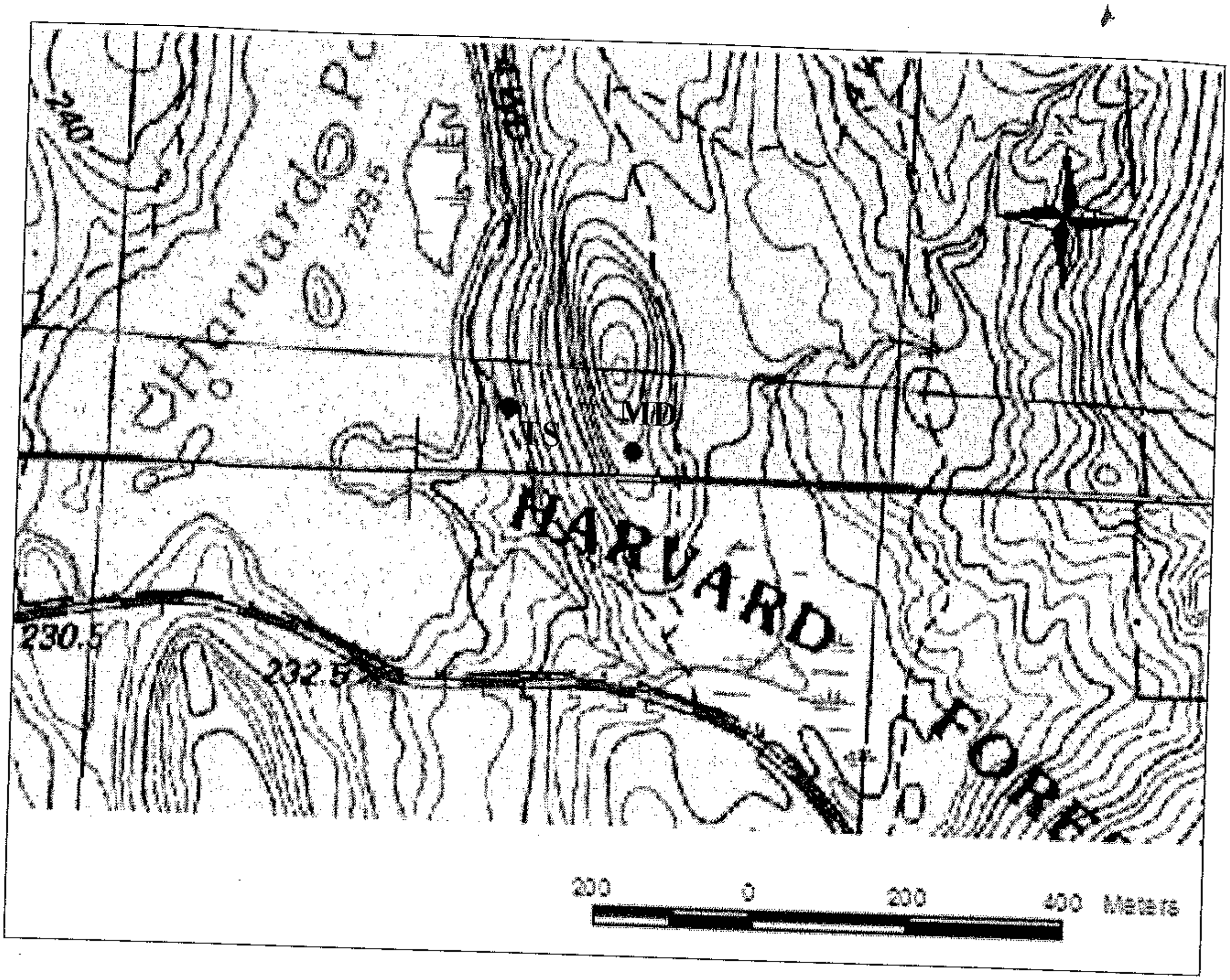
Map 8. Warwick State Forest (WSF).



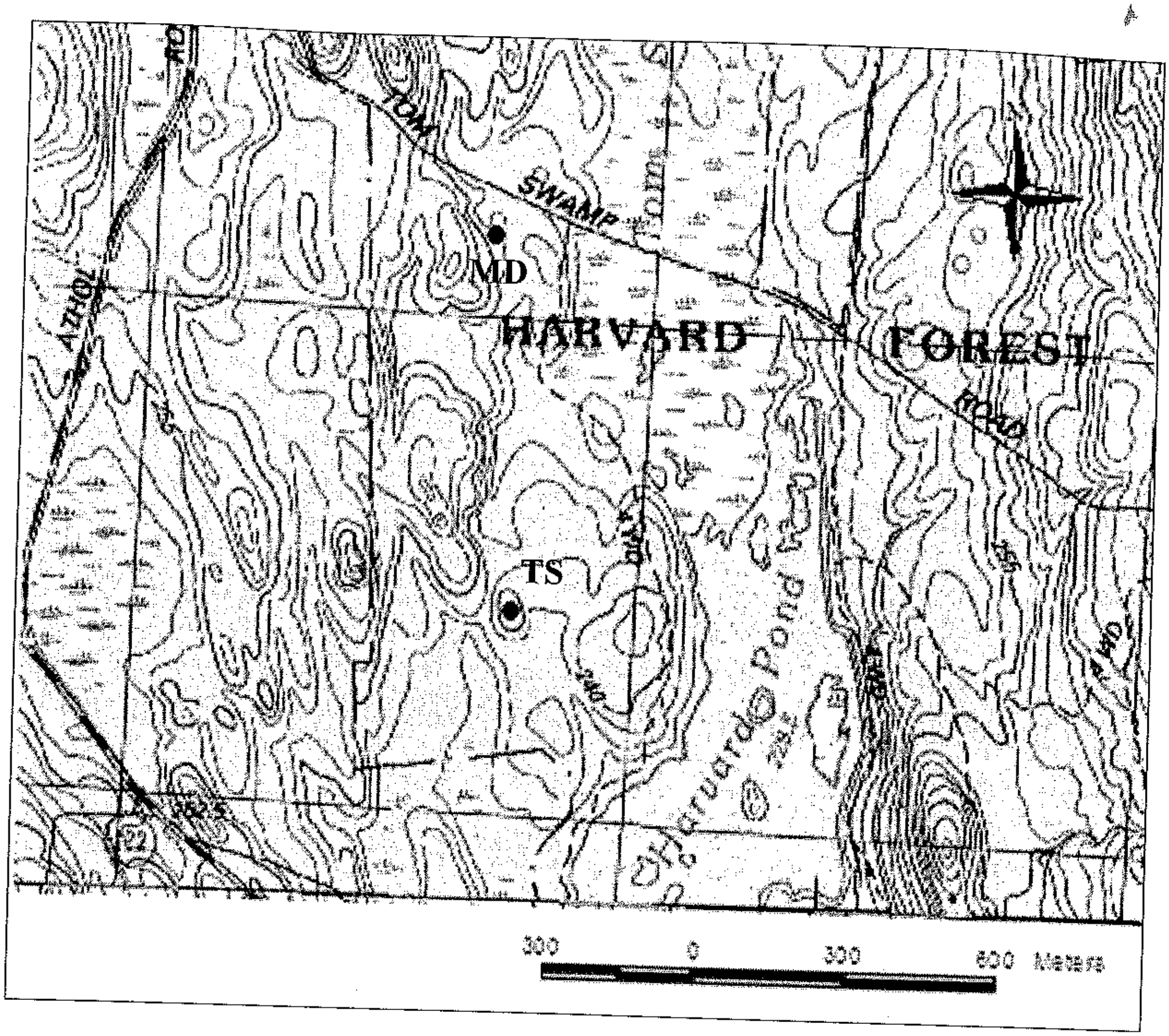
Map 9. Northfield State Forest (NSF).



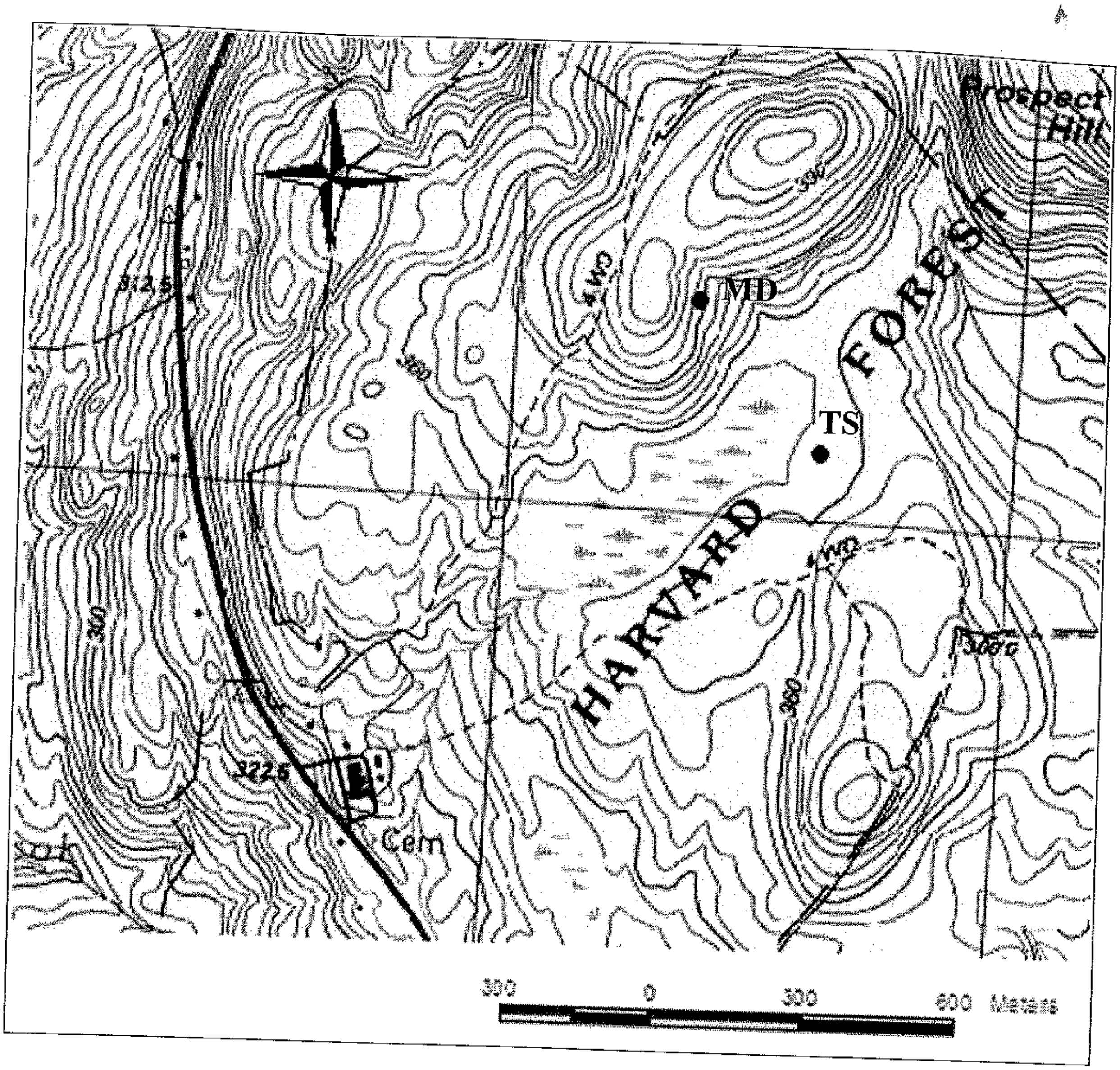
Map 10. Mount Grace State Forest (MG).



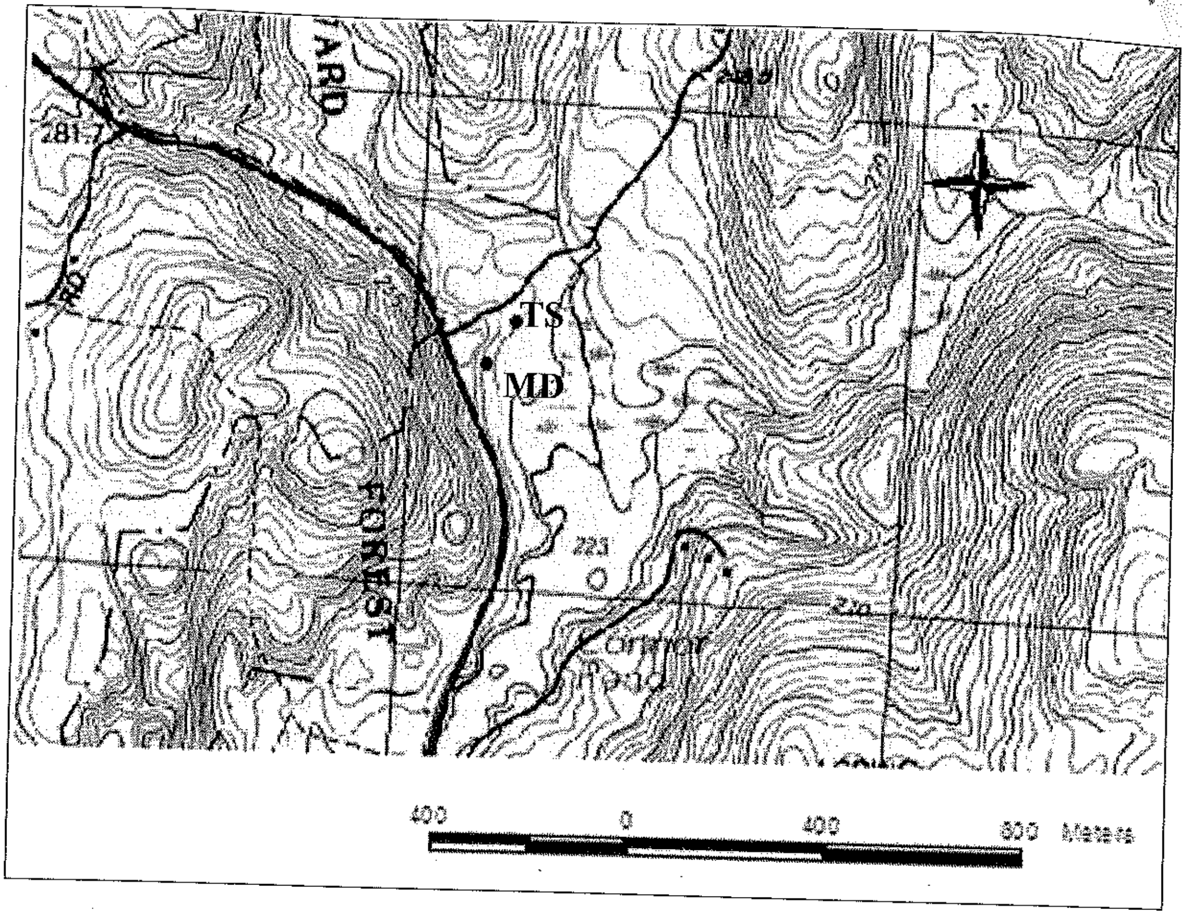
Map 12. Harvard Forest – Tom Swamp Site 1 (TS1).



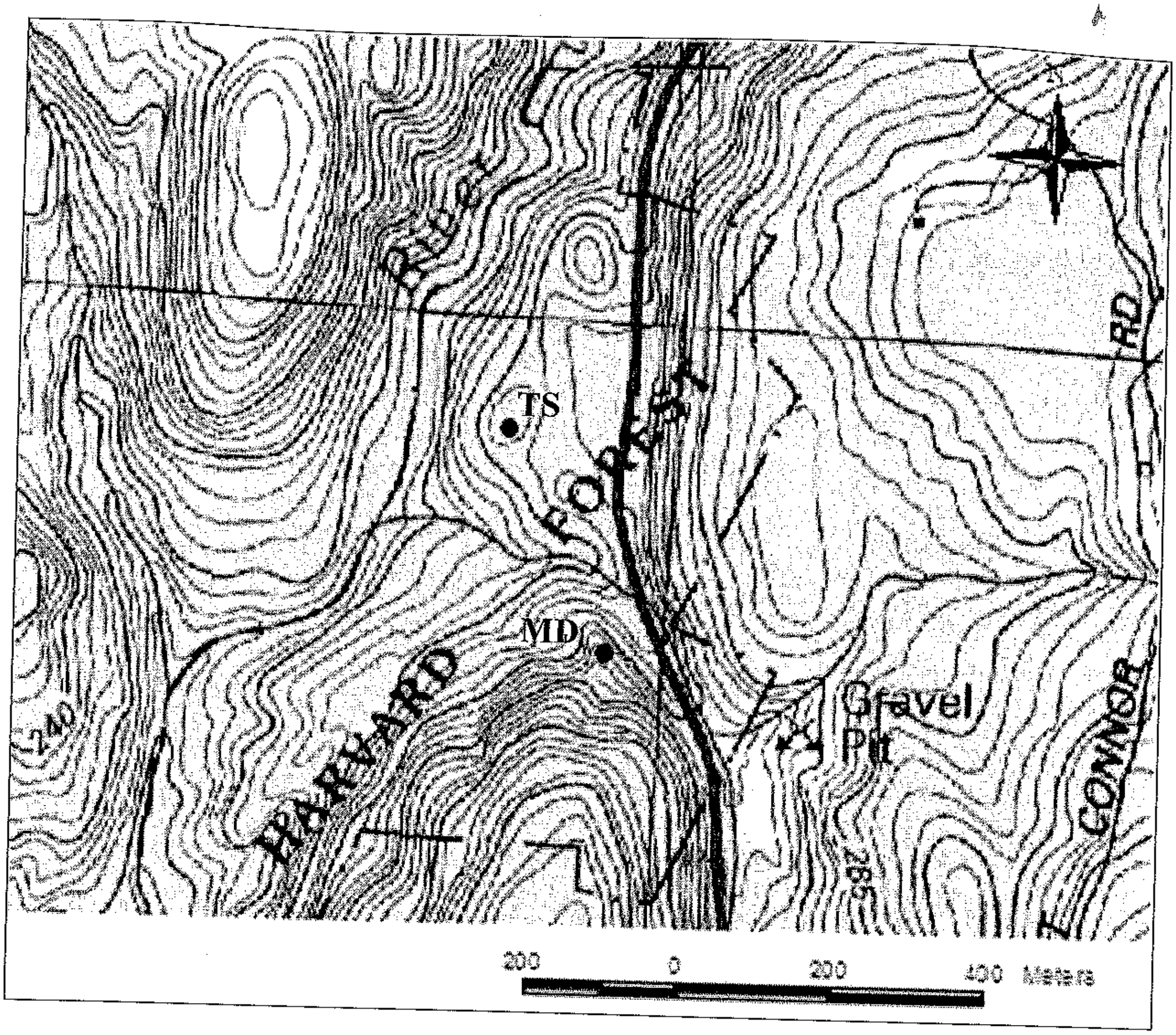
Map 11. Harvard Forest – Tom Swamp 2 (TS2).



Map 13. Harvard Forest – Prospect Hill (PH).



Map 14. Harvard Forest – Slab City Site 1 (SC1).



Map 15. Harvard Forest – Slab City 2 (SC2).

CHAPTER 3

Extended Discussion

This chapter is intended as an extended discussion of the study presented in chapter 2. Potential reasons for the differences in results obtained from this study of the relative abundance of eastern red-backed salamanders (*Plethodon cinereus* Green) in north-central Massachusetts and my earlier study of the relative abundance of *P. cinereus* at the Harvard Forest are discussed in this chapter. In addition, I examine the differences in the relative abundance of *P. cinereus* during the eight rounds of artificial cover object (ACO) monitoring from the middle of June through the beginning of November. There is also a brief section in this chapter devoted to general observations on the natural history of *P. cinereus*. Finally, I discuss areas which warrant future research concerning the ecological roles of *P. cinereus*.

Comparisons between Results at Harvard Forest and North-central Massachusetts

The lack of a difference in the relative abundance of *P. cinereus* in hemlock-dominated forests and mixed deciduous forests in north-central Massachusetts conflicts with an earlier study at the Harvard Forest, which found a higher relative abundance of *P. cinereus* in hemlock-dominated forests than mixed deciduous forests in three of four seasons (Mathewson in review). This may be partially explained by differences in the overstory tree composition of mixed deciduous forests at Harvard Forest versus the overall north-central region of Massachusetts. The average relative abundance of oak species within mixed deciduous forests at Harvard Forest was 56%, while in all other mixed deciduous forests in north-central Massachusetts oak only accounted for 33% of the total basal area of the stand. The species replacing oak were primarily black birch (*Betula lenta* L.), American beech (*Fagus grandifolia* Ehrh), and eastern hemlock (*Tsuga canadensis* (L.) Carr.). There was no difference in the relative abundance of red maple (*Acer rubrum* L.) and eastern white pine (*Pinus strobus* L.). Qualitatively, the CWD of black birch, American beech, and eastern hemlock seems to have more crevices and retain more moisture than the CWD of oak species, perhaps creating better habitat for *P. cinereus*. There may also be a difference in litter quality resulting in a difference in the quality or abundance of potential *P. cinereus* prey. It is also possible that there is less soil moisture in mixed deciduous forests with a higher relative abundance of oak species.

In the plots within Harvard Forest in this current study of north-central Massachusetts, the relative abundance of *P. cinereus* was higher in hemlock-dominated plots, though not significantly (one-way ANOVA; F = 3.41; df = 8; p = 0.107). In two of the sites at Harvard Forest (Slab City 1 (SC1) and Tom Swamp 1 (TS1)) the relative abundance of *P. cinereus* was more than four times greater in hemlock-dominated forest than in mixed deciduous forest. In the other two sites (Prospect Hill (PH) and Tom Swamp 2 (PH)), however, there was little difference between the relative abundance of *P. cinereus* in the two forest types. Interestingly, average soil pH in both hemlock-dominated plots with substantially higher relative abundance of *P. cinereus* was 3.8, while the average soil pH in both hemlock-dominated plots in which there was little difference in the relative abundance of *P. cinereus* was 3.6. This again illustrates how a soil pH below 3.7 can negatively affect the relative abundance of *P. cinereus*. It is also interesting that more observations of juvenile eastern red-spotted newts (*Notophthalmus* *viridescens viridescens* Rafinesque) were made in the hemlock-dominated plots at TS2 and PH than in SC1 or TS1, although the sample sizes were extremely small (n = 13).

Fluctuations in Red-backed Salamander Counts

The lowest counts of *P. cinereus* under ACOs occurred in the second week of August, while the highest counts were recorded in the final two rounds of monitoring (September 28th to October 6th and October 18th to November 4th) (Figure 2). These results are consistent with other ACO studies in Massachusetts, which found that *P. cinereus* were observed most commonly in the spring and fall (Brooks 2001; Mathewson 2004; Mathewson in review). During the hot and dry summer months red-backs are generally found in sub-surface retreats rather than on the surface of the soil (Petranka 1998). In addition, nesting females are rarely on the surface while attending egg masses during the summer (Ng and Wilbur 1995).

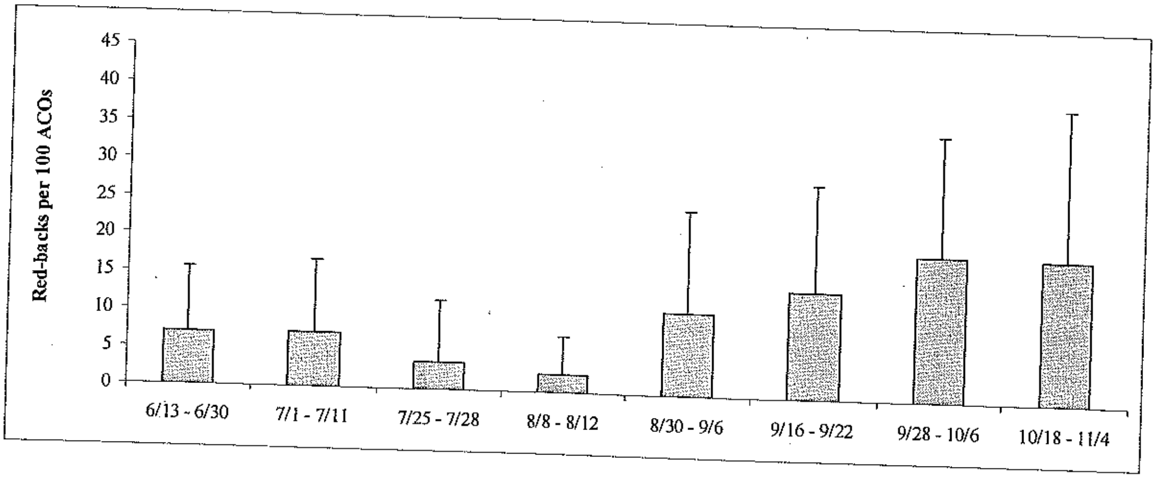


Figure 1. Relative abundance of *P. cinereus* in north-central Massachusetts as measured by artificial cover object (ACO) monitoring over eight rounds of monitoring from June 13, 2005 to November 4, 2005

Natural History Notes

The first hatchling was observed on September 28, 2006 measuring 17mm. This suggests that ovipositing took place probably between mid-June and mid-July, which coincides with past studies of *P. cinereus* nesting in Massachusetts (Lynn and Dent 1941). Only two of 250 observations of *P. cinereus* were of the lead-backed phase. These observations took place in hemlock-dominated plots at SC1 and Erving State Forest 2 (ER2). This percentage is even lower than the 3% frequency observed within Harvard Forest (Mathewson 2004). Two *P. cinereus* were not observed under the same ACO until September 20th. After this date two red-backs were observed under the same ACO 15 times, and three red-backs were observed under the same ACO twice, suggesting that there may be a behavioral shift in tolerance of conspecifics at different times of the year.

The heaviest *P. cinereus* specimen, observed in the mixed deciduous plot at ER2, weighed 1.60 g (snout-vent length (SVL): 45mm; total length (TL): 90mm) and was identified as a female. The red-back with the longest SVL was observed in the plot in mixed deciduous forest at Northfield State Forest (NSF) and had the following measurements: weight: 1.11g; SVL: 50mm; TL: 85mm; sex: unknown. Finally, the red-back with the longest TL was a male observed in the plot in mixed deciduous forest at Mount Grace State Forest (MG) with the following measurements: weight: 1.55g; SVL: 45mm; TL: 95mm.

Future Red-backed Salamander Research

Despite their abundance little is known concerning the ecological role of *P.*

cinereus in the forest (Wyman 1998). In the thirty plots in this study the relative abundance of *P. cinereus* varies twenty-five fold. This gradient might be used to examine relationships between the relative abundance of *P. cinereus* and the relative abundance of potential predator and prey species. There is initial evidence that *P. cinereus* may have a role in determining the density of invertebrates both directly and indirectly (Wyman 1998; Rooney et al. 2000). Although no previous studies have yet explored this area it also seems likely, given their abundance and high protein content, that the abundance of *P. cinereus* could impact the abundance of vertebrate predators. A study of the relative abundance of vertebrates, that is, birds, small mammals and reptiles, in the plots in this study would be extremely worthwhile. It would also be interesting to explore whether the abundance of juvenile *N. v. viridescens* may have an impact on the relative abundance of *P. cinereus*.

Another study which would be extremely worthwhile would be to assess the relative abundance of *P. cinereus* in old-growth hemlock-dominated forests in the Berkshire Hills and Taconic Mountains in western Massachusetts. In old-growth forests in western North America the relative abundance of terrestrial salamanders has been found to be significantly higher than in younger forests due to structural and microclimatic reasons (Welsh and Lind 1988; Dupuis et al. 1995). It would also be useful to examine the relative abundance of *P. cinereus* in other forest types, for example eastern white pine stands. This forest type is very common in this area, and it would be interesting to be able to compare the relative abundance of *P. cinereus* in a forest type which likely has low soil pH, but differs in many other structural and climatic ways from hemlock-dominated forest

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