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EFFECTS OF SELECTION LOGGING ON AMPHIBIAN DIVERSITY AND ABUNDANCE IN SHADE-TOLERANT HARDWOOD FORESTS OF ALGONQUIN PROVINCIAL PARK, ONTARIO

A Thesis

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of

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by

LISA ENRIGHT

In partial fulfilment of requirements

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ABSTRACT

EFFECTS OF SELECTION LOGGING ON AMPHIBIAN DIVERSITY AND ABUNDANCE IN SHADE-TOLERANT HARDWOOD FORESTS OF ALGONQUIN PROVINCIAL PARK, ONTARIO

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Despite amphibians' widely acknowledged importance in forest ecosystems, they are rarely included in forest management plans. Very little is known about the effects of, or amphibian response to, timber management. To determine whether and if so, how selection logging affects amphibians in shade-tolerant hardwood forests, I compared amphibian habitat concurrently with amphibian diversity and abundance in managed (logged) and unmanaged (unlogged) forest stands in Algonquin Provincial Park, Ontario. Selection logging significantly altered aspects of shade-tolerant hardwood forest habitat on which amphibians are known to depend. However, with the exception of American Toads (*Bufo americanus*) that were more abundant in managed stands, the overall diversity and abundance of amphibians did not differ significantly between managed and unmanaged areas. Therefore, I concluded that selection logging does not alter hardwood forest habitat to the degree that it negatively affects amphibian diversity or abundance. Implications of this conclusion are discussed.

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INTRODUCTION

For the past 10 to 15 years, there has been much concern and controversy over apparent and widely reported amphibian population declines (Beebee 1992; Blaustein 1994; Blaustein and Wake 1990; Blaustein *et al.* 1994b; Dunson *et al.* 1992; Green 1996; Pechmann *et al.* 1991; Pechmann and Wilbur 1994; Vitt *et al.* 1990; Wake 1991). Much of the concern stems from the generally accepted, but untested, assumption that amphibians function as bioindicators and may signal widespread, anthropogenically induced, environmental degradation (e.g. Blaustein 1994 and references cited therein, and Vitt *et al.* 1990; but also see Dunson *et al.* 1992, and Pechmann and Wilbur 1994). Controversy, on the other hand, centers around the use of anecdotal data to support claims of local or global declines and extinctions that are purported to be distinct from the more general biodiversity crisis.

Without experimental evidence or extensive data from long-term population studies, it is difficult, if not impossible, to distinguish between "natural," stochastic population fluctuations and those that are anthropogenically induced (Blaustein 1994; Pechmann *et al.* 1991; Pechmann and Wilbur 1994). Nevertheless, recent investigations suggest that anthropogenic disturbances are primarily responsible for the majority of documented amphibian population declines. Observed declines have been attributed to: high levels of UV-B radiation (Blaustein *et al.* 1994a); introduction of exotic species (Bradford 1991); habitat destruction and alteration (Blaustein 1994; Blaustein *et al.* 1994b; Green 1996;

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Wake 1991); forest fragmentation (Laan and Verboom 1990; Reh and Seitz 1990); increased environmental acidity (Dunson *et al.* 1992; Freda 1986); and logging (deMaynadier and Hunter 1995).

Although unable to elucidate concrete evidence for causal mechanisms behind amphibian population declines, this controversy has nevertheless brought amphibians to a more prominent level of recognition among biologists, resource managers and the public, and has driven much of the recent research into amphibian ecology and conservation biology in both terrestrial and aquatic ecosystems. Researchers are now investigating more thoroughly the effects of, and amphibian response to, various anthropogenic disturbances, while resource managers are demanding that ecologists provide them with the information necessary to include amphibians (as well as other non-game wildlife) in habitat management plans (deMaynadier and Hunter 1995; Dunson *et al.* 1992; Riley and Mohr 1994).

Much of the North American land base historically dominated by forest ecosystems has been reduced, degraded and fragmented as land was cleared and developed for human use. Although some areas are now completely devoid of forest, a large proportion of public and private lands are managed for timber (e.g. Anderson *et al.* 1990; Riley and Mohr 1994; Schmiegelow *et al.* 1997). In light of the accumulated evidence suggesting that amphibians are declining in response to anthropogenic disturbances, and at a time when ecologists, foresters, government agencies and private landowners are attempting to integrate timber management with ecological interests and habitat conservation (Anonymous 1995; Bormann *et al.* 1974; Bormann and Likens 1967; Gillis 1990; Hansen *et al.* 1991; Likens *et al.* 1978; Riley and Mohr 1994; Schmiegelow *et al.* 1997), recent research efforts have focused on determining the effects of timber management on amphibians, and amphibian responses to logging in different forest types (deMaynadier and Hunter 1995).

The importance of amphibians in forest ecosystems is frequently acknowledged by ecologists investigating the effects of timber management on terrestrial amphibians (e.g.

Bennett *et al.* 1980; Clawson *et al.* 1997; DeGraaf and Yamasaki 1992; Pais *et al.* 1988; Petranka *et al.* 1993, 1994; Pough *et al.* 1987). These investigators cite a number of original studies that show amphibians to be relatively abundant over small areas of the forest floor (Heatwole 1962; Jaeger 1980) and to comprise a highly significant component of total vertebrate biomass in the hardwood forests of northeastern North America (Burton and Likens 1975a). In addition, evidence suggests that amphibians are important as both prey and predator: they are efficient secondary producers (Burton and Likens 1975b; Pough 1980), and they are top predators of the decomposer food web (Bellocq, Kloosterman and Smith, unpublished manuscript; Fraser 1976; Jaeger 1972). By preying on populations of soil invertebrates, amphibians are thought to regulate populations of organisms responsible for organic decay (deMaynadier and Hunter, 1995 summarize thoroughly the most commonly cited literature on this topic).

Despite these ecological roles, amphibians are rarely included in habitat management plans (Bury *et al.* 1980; Dunson *et al.* 1992; Jones 1986). When considered, they are often stereotyped. For example, Anderson *et al.* (1990) state that timber management strategies to maintain or enhance fish habitat ensure the protection of most riparian areas, and therefore most amphibian habitat. Although this might be true for many species inhabiting northeastern hardwood forests, it is not true of all amphibians. Some terrestrial amphibians such as the Red-backed Salamander (*Plethodon cinereus*) rely solely upon microhabitats (e.g. downed logs, root systems and leaf litter) on the forest floor for survival and reproduction. Others such as the Wood Frog (*Rana sylvatica*) and Spring Peeper (*Pseudacris crucifer*) use upland forest microhabitats for foraging and refuge, but rely upon ephemeral pools within or adjacent to forests for egg laying and larval development (Conant and Collins 1991; Cook 1984; Tyning 1990).

That amphibians are generally ignored by most wildlife managers is as much a reflection of the fact that amphibians are inconspicuous (small, nocturnal, fossorial, arboreal and/or silent) inhabitants of forest ecosystems as it is a reflection of the general

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lack of experimental evidence necessary to explicitly quantify the importance of amphibians in forest ecosystems, and a lack of knowledge of mechanisms regulating amphibian populations at both the larval and adult stages (Wilbur 1980; deMaynadier and Hunter 1995). This lack of information has theoretical and practical implications for the development of ecologically sound management plans for forest ecosystems. Clearly, ecologists need to provide forest managers with more information about the effects of timber management on amphibians, and of amphibian response to these disturbances. Only with this level of knowledge and understanding will it be possible to include amphibians in the balance of conflicting ecological and economic values associated with timber management in North America (Cumming *et al.* 1994; Dunson *et al.* 1992).

deMaynadier and Hunter (1995) emphasize this perspective in their review of the available literature on the relationships between forest management and amphibian ecology. Although much (relatively speaking) is known of the effects of clearcutting on amphibian populations in both coniferous and deciduous forests, basic information and mechanistic understanding are lacking in many significant areas. For example:

(1) Their review of the literature shows that clearcutting in both deciduous and coniferous forests has a negative impact on amphibian populations: amphibian abundance in control forest stands is, on average, 3.5 times greater than that observed in forested areas that had been recently clearcut. However, deMaynadier and Hunter (1995) also stress that we still do not know how amphibians respond to disturbances of this magnitude (Ash and Bruce 1994; Petranka 1994; Petranka *et al.* 1993). Do they aestivate underground until more suitable environmental conditions arise (Feder 1983), or do they emigrate from the site (literature reviewed by deMaynadier and Hunter 1995)? Lower survivorship and abundance in areas adjacent to clearcut stands indicate that salamanders perish on clearcut sites (Ash 1988; Raymond and Hardy 1991).

(2) Generalizations of the effects of timber management on amphibians are being drawn when only one species or specialized group of amphibians is studied (e.g. Petranka *et al.*

1993, 1994), or when trends observed for a particular amphibian assemblage are driven by only one species. Of 18 papers written specifically on the effects of clearcutting on amphibians, 16 focused on salamanders (15 of these focused on Plethodontids), and only 9 of the 18 studies included anurans. deMaynadier and Hunter (1995) suggest that evaluations of the impacts of timber harvesting be made on a species by species basis, in light of the very different life history strategies exhibited by various species of frogs, toads and salamanders.

(3) Knowledge of the nature of the effects of partial, or uneven-aged, harvesting protocols such as selection or shelterwood logging on amphibian populations in the shade-tolerant hardwood forests of northeastern North America is also lacking. To date, the effects of these harvesting protocols on amphibians have been virtually unstudied (deMaynadier and Hunter 1995), despite the fact that these management strategies are consistently recommended and used in forest management plans for northern hardwood forests (e.g. Anderson *et al.* 1990; deMaynadier and Hunter 1995; OMNR 1983). Ecologists studying the effects of forest age on amphibian diversity and abundance have suggested that it is not the age of the trees in the forest that is important to amphibians in and of itself, but the microhabitats characteristic of older, mature forests (Welsh 1990). Therefore, partial harvests that maintain some of the structural integrity of uneven-aged forests (e.g. downed woody debris, leaf litter depth, canopy cover) may provide sufficient suitable habitat for a variety of amphibians (but see Petranka *et al.* 1993). To my knowledge, no research has, as yet, been conducted on this topic even though this information would be invaluable to forest managers when predicting impacts of even- and uneven-aged management strategies in attempts to balance ecological and economic interests (deMaynadier and Hunter 1995).

(4) Almost nothing is known of the effects of timber management and associated activities (e.g. road building, site preparation) on breeding populations of amphibians that are either facultative or obligate users of naturally occurring ephemeral pools for egg laying

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and larval development. Amphibians also use roadside pools created by logging road construction, but it is not known whether these pools act as population sources or population sinks for the breeding amphibians that use them (deMaynadier and Hunter 1995).

Selection logging is a widely used uneven-aged management strategy for shade-tolerant northern hardwood forests of northeastern North America. It involves the removal of a predetermined cumulative basal area (m²/ha) of individual poles or small groups of pole (9 cm < diameter < 24 cm), saw (24 cm < diameter < 50 cm), and occasionally mature (diameter > 50 cm) crop trees for timber production on a rotational basis. At the same time, dead and/or decaying trees are removed to create openings in the canopy, which helps to reduce competition among the remaining crop trees for light and nutrients (Anderson et al. 1990). Selection logging protocol is designed, and assumed to mimic as closely as possible, natural disturbances such as windthrow, small fires and insect outbreaks (Anonymous 1995); however, this assumption remains to be tested.

Because selection logging removes only individual or small groups of trees at a time, the structural integrity of small areas of the forest is essentially left intact (albeit disturbed), and mature trees in managed hardwood forest stands are maintained at an age of about 100 to 150 years. Bonin (1991), Petranka et al. (1993, 1994) and Pough et al. (1987) suggest that amphibian populations recover from clearcutting in northern hardwood forests that have reached ages of 30-60, 60-120 and 60 years, respectively, but it is not known whether the recovery of amphibian populations is due specifically to forest age or to the recovery of microhabitats characteristic of these older forests. For example, both Pough et al. (1987) and Bonin (1991) suggest that recovery of the leaf litter layer and soil-litter interface are prerequisites to the recovery of amphibian populations in clearcut northern hardwood forest stands. Pough et al. (1987) also show that minor disturbances such as selective cuts for firewood do not seem to have negative impacts on Red-backed Salamander or Red-spotted Newt (*Notophthalmus viridescens*) populations. It therefore

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seems possible that selection logging, which maintains some leaf litter, downed woody debris, and canopy cover, may have little potential to affect amphibians adversely. However, the following aspects of selection logging protocol, unique to this management strategy, suggest that this type of timber management could also have negative impacts on amphibian populations inhabiting managed stands.

(1) Selection logging has the potential to skew the age structure and quality of forest stands in favour of younger, crop quality trees. Because this management strategy selects for fast-growing trees approximately 150 years of age and younger (Anderson *et al.* 1990; OMNR 1983), it is expected that the cumulative basal area of logged forest stands will be less than that in unmanaged forest stands (i.e. there will be fewer mature trees greater than 50 cm diameter). Removal of "over mature" crop trees, as well as dead, dying, diseased, or otherwise economically nonviable trees from a forest stand is expected to result in fewer large pieces of standing and downed woody debris that are moderately to well decayed. Major changes in the amount and size of downed woody debris in various states of decay could result in lower amphibian abundance in managed forest stands. Salamander abundance correlates positively with the amount of downed woody debris in forests of northwestern (Dupuis *et al.* 1995) and northeastern North America (Petranka *et al.* 1994). Positive associations of salamander abundance with larger logs that are moderately to well decayed have also been observed (Heatwole 1962, Petranka *et al.* 1994).

(2) At the stand scale, canopy reduction could cause an increase in the amount of incident radiation that reaches the forest floor. If incident radiation were to increase significantly, then litter, soil and water temperatures would increase, as would evaporation rates, resulting in a decrease in soil and litter moisture content, as well as in the size and duration of naturally occurring and roadside ephemeral pools over time. Changes in soil and litter temperature and moisture content could result in a corresponding change in understory vegetation type, density and composition (see Bury 1983). It is not known to what extent partial canopy reduction might affect microhabitat variables such as litter depth

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and understory vegetation density. Studies are needed to examine these relationships and to relate changes in amphibian fauna directly to changes in habitat variables between managed versus unmanaged forest stands. However, it is known that terrestrial salamanders are spatially and temporally restricted to areas with sufficient moisture for survival and reproduction (Duellman and Trueb 1986; Feder 1983; Heatwole 1962; Jaeger 1972, 1980; Spotila 1972). High temperatures combined with dry microhabitats interfere with respiration and foraging opportunities (Feder 1983; Spotila 1972). Therefore, any disturbances affecting ambient temperatures and moisture availability in microhabitats used by amphibians have the potential to affect amphibian diversity and abundance.

(3) Disturbances associated with road construction and the operation of heavy machinery (e.g. skidders) could alter local topography, and affect the number, size and distribution of ephemeral pools which are used by the majority of amphibians for breeding. Wood Frogs (Berven and Grudzien 1990) and Yellow-spotted Salamanders (Stenhouse 1985) show a high degree of breeding site fidelity and both (Berven 1982, and Whitford and Vinegar 1966, respectively) will return to their traditional breeding pool after being displaced to an alternate site. This suggests that any alteration of the number and distribution of ephemeral pools, as well as the creation of roadside pools through logging road construction, could affect the extent to which these pools are used by local populations of amphibians. Sediment loading and increased turbidity within these roadside pools could adversely affect the development rate of egg masses. Reduced canopy cover associated with roadside pools (see Patric 1976) could: increase amphibian (i.e. egg, larval and adult) exposure to UV-B radiation (Blaustein et al. 1994a); increase temperature and evaporation rates of roadside ephemeral pools; and decrease roadside ephemeral pool duration (deMaynadier and Hunter 1995). It is not known whether roadside ephemeral pools act as population sources or sinks for the populations of breeding amphibians that use them.

It is difficult to predict whether, and if so by what mechanism(s), selection logging affects amphibians, in part because the effects of selection logging on hardwood forest

habitat have not been quantified. In many areas, selection logging is conducted in the late fall and winter, when amphibians are inactive underground or under logs and leaf litter on the forest floor. Logging roads are constructed and maintained during the summer months, when it is often too hot and dry for amphibians to be moving about on the forest floor. It is therefore most likely that selection logging will affect amphibian populations indirectly, by altering the availability and quality of habitat necessary for amphibians to survive (forage, find refuge, disperse) and/or reproduce (Dupuis *et al.* 1995).

The general aim of this investigative research was to address some of the issues raised by deMaynadier and Hunter (1995). In particular, my goal was to determine the effects of one type of partial harvest; that is, selection logging, on amphibians in general, and on individual species for which I could collect enough data for analysis. In part, I attempted to focus my efforts on forest-dwelling anurans that were facultative users of ephemeral breeding pools. By comparing a wide array of habitat variables known to be important to amphibians, concurrently with the diversity and abundance of 11 species of frogs, toads and salamanders in logged (managed) and unlogged (unmanaged) forest stands in Algonquin Provincial Park, Ontario, my goal was to determine whether, and if so, by which mechanism(s), selection logging affects amphibians in shade-tolerant hardwood forests. To my knowledge, this is the first study of the effects of partial harvesting on amphibians in northeastern North America. While the results of this research will not be specifically applicable to amphibian populations in other areas because of differences in elevation (cf. Petranka *et al.* 1993 and 1994), soil type, species assemblages and so on, they will be broadly applicable to timber management protocols involving partial harvests that are implemented in the northern hardwood forests of northeastern North America.

METHODS

Study Area

This research was undertaken between 1 May and 1 November of 1996 and 1 May and 31 August of 1997, in the west side of Algonquin Provincial Park, Ontario, Canada, and was based out of the Wildlife Research Station (WRS) at Sasajewun Lake (45°35' 78°32'). The moderately rolling ridges of this glaciated upland area range in elevation from approximately 366 m to 585 m above sea level and are on average 200 m above the surrounding land. Because of its higher elevation, the west side of Algonquin is typically cooler and wetter than the surrounding area: the Algonquin highlands receive an annual average of 100 cm of precipitation (33 percent as snow) and have only 80-90 frost free days per year, whereas the surrounding areas receive only 90 cm of precipitation annually (26 percent as snow) and have a growing season of about 100-110 frost free days (Anderson *et al.* 1990, Strickland 1993).

Moulded and dumped glacial till (silty sands and sandy loams) over granitic bedrock supports shade-tolerant hardwood forests comprised primarily of Sugar (Hard) Maple (*Acer saccharum*), American Beech (*Fagus grandifolia*), Yellow Birch (*Betula alleghaniensis*) and Eastern Hemlock (*Tsuga canadensis*). Commonly associated hard- and softwoods include species such as Black Cherry (*Prunus serotina*), Ironwood (*Ostrya virginiana*), Black Ash (*Fraxinus nigra*), Red Maple (*Acer rubrum*), White Pine (*Pinus strobus*), White Spruce (*Picea glauca*) and Balsam Fir (*Abies balsamea*). This forest type characterizes forests in the Great Lakes-St. Lawrence forest region of Ontario, Québec, and northern New Brunswick (Hosie 1990), as well as the northern hardwood forests of the north eastern United States (Anderson *et al.* 1990; Bormann *et al.* 1970; OMNR 1983).

Prior to 1974, shade-tolerant hardwood forest stands in Algonquin were managed using a combination of light highgrading for Yellow Birch and White Pine, and diameter limit cutting (OMNR 1983). Since the implementation of the Park's Master Plan in 1974

(OMNR 1974), shade-tolerant hardwood forest stands have been managed under a standardized selection system of silviculture (Anderson *et al.* 1990; OMNR 1983). At present, just under 80 percent of the total Park area (7,725 km²) is managed under selection, shelterwood or clearcut silvicultural systems. Shade-tolerant hardwoods represent approximately 50 percent of the productive forest in Algonquin (249,140 ha) and a small percentage of this area is logged each year, on a rotational basis (OMNR 1983).

With the inception of the Park's Master Plan in 1974 (OMNR 1974), forest stands along the Highway 60 corridor of the Park were included within a Development Zone. In this zone, small areas were developed (or had already been developed) as campgrounds and hiking trails for public use, but the majority of the forest stands were left undisturbed. Although few logging records exist for forest stands in the Park prior to 1960, it is likely that these forest stands had not been disturbed or logged for a significant period of time prior to the implementation of the Park's Master Plan, because of the Park's desire to limit potential conflicts between forest managers and members of the public. Aside from areas used for camping or hiking, forest stands along the Highway 60 corridor likely have not been logged or otherwise disturbed for at least the past 40 to 50 years, and probably longer (Mihell, personal communication).

Study Sites

To determine whether, and if so, how (i.e. by altering which aspects of amphibian habitat) selection logging affects amphibian diversity and abundance in shade-tolerant hardwood forest habitat, I compared amphibian diversity and abundance concurrently with amphibian habitat in 10 forest stands actively managed under the selection logging system, and 10 unmanaged forest stands within the Development Zone of the west side of Algonquin Provincial Park (Table 1). Managed and unmanaged forest stands were chosen at random from large areas of contiguous forest stands that were: known to be accessible in late April through early May by a 4 x 4 truck and/or an all terrain vehicle (ATV); known to

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be comprised of at least 70 percent shade-tolerant hardwood species and a minimum of 60 percent Sugar Maple; and known to have similar disturbance histories, up to the point of selection logging (Table 1).

All 10 unmanaged forest stands were randomly chosen from a large area (approximately 36 km^2) of accessible, contiguous forest stands along the Highway 60 corridor of Algonquin (Figure 1). However, it was difficult to find a similar large, contiguous block of accessible, managed forest stands with identical logging histories from which 10 could be chosen at random. It was therefore necessary to choose the 10 managed forest stands from two areas: 5 forest stands chosen from the Sunday Lake Road area (approximately 16 km^2 total area) were logged in 1966-1967 and again in 1993-1994; and 5 forest stands chosen from the Martin Lake Road area (approximately 18 km^2 total area) were logged in 1965-1966 and again in 1994-1995. The Sunday Lake Road and Martin Lake Road areas of Algonquin are approximately 19 km apart from each other and each is approximately 13 km and 16 km, respectively, from the unmanaged forest stands along the Highway 60 corridor (Figure 1). Within each of the managed and unmanaged areas surveyed in 1996 and 1997 (Table 1), forest stands were a minimum of 150 m apart, and no forest stand was greater than 4 km from any other.

Throughout this research, managed and unmanaged forest stands were surveyed in pairs to control for weather fluctuations between surveys (Figure 1). From 1 May to 1 November 1996, 5 forest stands in the Sunday Lake Road area of the Park (stands A through E; Figure 1) and 5 unmanaged forest stands along the Highway 60 corridor (stands a through e; Figure 1) were surveyed. The remaining 5 pairs of managed stands (F through J; Figure 1) in the Martin Lake Road area and unmanaged stands (f through j; Figure 1) along the Highway 60 corridor were sampled between 1 May and 31 August 1997. This way, I was able to sample forest stands in the Sunday Lake and Martin Lake Road areas of the Park 2-3 years after they were logged, under the assumption that the effects of selection

logging on amphibian habitat, diversity and abundance would be of greatest magnitude, and therefore most easily detected and quantified, soon after logging.

Study Species

A total of 16 species of amphibians are known from Algonquin Provincial Park (Strickland and Rutter 1992). Of these, I expected to encounter a maximum of 12 species during surveys of amphibian habitat within the shade-tolerant hardwood forests of the west side of Algonquin (Table 2). The remaining 4 species of amphibians are either found exclusively on the east side of Algonquin Park (Strickland and Rutter 1992), or are found in habitat types not adequately sampled by the survey methods employed. Survey methods (summarized below in Parts III and IV) were designed to capture all amphibian species present during each observable stage in their life cycle (i.e. breeding adults, egg masses, larvae, juveniles and non-breeding adults). However, data collection and analysis focused on Red-backed Salamanders, Spring Peepers, Wood Frogs and American Toads (*Bufo americanus*). Red-backed Salamanders rely on the availability of moist, decaying logs and forest debris for breeding, foraging, refuge and dispersal, whereas Wood Frogs and Spring Peepers rely on these habitats (in part) for refuge, foraging and dispersal only. Both Wood Frogs and Spring Peepers require ephemeral pools and permanent ponds for breeding habitat. American Toads on the other hand, can survive and breed in drier sites, and need only shallow ephemeral pools or ditches for egg laying and tadpole development (Conant and Collins 1991; Cook 1984; Tyning 1990). All of these species are easily surveyed and counted at many stages in their lifecycle, and because each species relies on different aspects of hardwood forest habitat, selection logging has the potential to affect these species to different degrees and at different stages in their life cycle. By focusing data collection and analysis on species whose natural and life histories are known to vary, I was able to investigate whether, and if so, how selection logging affects amphibians as a group. I was then able to use this information to suggest whether selection logging would be

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expected to affect other species of amphibians with similar natural and life histories that were not detected in sufficient numbers for statistical analysis.

Survey Methods

I wished to characterize and compare the composition of amphibian communities in managed and unmanaged forest stands. To do this, I used a combination of several survey methods, modified from methods recommended by Heyer *et al.* (1994), to quantify the diversity and abundance of all amphibian species encountered, at each observable stage in their life cycle. Each type of survey was used to examine diversity and abundance in a particular type of habitat known to be of importance to different species or life stages of amphibians. Surveys of ephemeral pools were used to characterize the diversity and abundance of breeding adults, egg masses and larvae; quadrat surveys were used to quantify the abundance of Red-backed Salamanders in particular; and drift fence and pitfall trap surveys were used to quantify the abundance of amphibians moving about on the forest floor during the spring, summer and fall seasons (Figure 2). I also wished to quantify the habitat available to amphibians in managed and unmanaged forest stands to determine mechanisms by which selection logging affected the composition of amphibian communities. To this end, I quantified characteristics of each ephemeral pool surveyed; hardwood forest habitat (e.g. leaf litter depth, density of the understory, canopy cover) in each of the quadrats included in the survey; and soil temperature and moisture at each of the drift fence and pitfall trap arrays included in the survey. Survey methods used to characterize amphibian habitat, diversity, and abundance are explained in detail in the respective sections below.

Data Analysis

Each of the survey methods described in the sections below was designed to determine whether selection logging affects the abundance and diversity of amphibians in managed

and unmanaged forest stands. I used these methods to test the following null hypothesis: there is no difference in amphibian diversity and abundance in forest stands managed under selection logging relative to forest stands left undisturbed for at least 40-50 years.

Results of this research will be of importance to forest managers who wish to include amphibians in forest management plans, as well as those responsible for the formulation and/or revision of silvicultural practices and policies based on current ecological data. For these reasons, and because amphibian populations can fluctuate a great deal from year to year, I felt that a type II error (not rejecting the null hypothesis when it is false) was more costly than a type I error (rejecting the null hypothesis when it is true). To reduce the chances of committing a type II error, I used an alpha value of 0.10 for all analyses of amphibian data (Cohen 1988; Schmiegelow et al. 1997; Welsh and Lind 1995; Zar 1984). In all other cases; that is, in analyses of habitat data and of amphibian-habitat relationships, the conventional alpha value of 0.05 was used.

Prior to conducting each analysis, data were examined using the Kolmogorov-Smirnov test (Zar 1984) to determine whether there were any severe deviations from normality. Where possible, non-normal data were transformed using conventional transformations (Krebs 1989; Zar 1984) or non-parametric statistics were used. I did not examine the data for homogeneity of variances, because of the generally poor performance of these tests (Zar 1984), but assumed instead that normalizing the data would equalize the variances (Krebs 1989; Zar 1984). In all cases of repeated measure ANOVA analyses, abundance data were not normal and conventional transformations did not normalize the data. Box-Cox (Krebs 1989) and Taylor's Power Law (Southwood 1978) transformations were also attempted, but with no success in determining a common transformation to normalize the abundance data collected for each week of ephemeral pool, quadrat or drift fence surveys. ANOVA analyses are known to be robust to deviations from the assumptions of normality and homogeneous variances (Zar 1984) and I relied on this assumption when analyzing the abundance data. Univariate analyses were completed using Statview SE+, version 1.04

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(Abacus Concepts, Inc.) on a Macintosh Performa 5200 CD. Multivariate analyses were performed using NTSYS-pc, version 1.80 (Applied Biostatistics, Inc.) on a 386 IBM-compatible personal computer.

PART I: VARIATION BETWEEN STUDY SITES AND SURVEY YEARS

Observed differences in amphibian habitat, diversity and abundance between managed and unmanaged forest stands surveyed in successive years cannot be attributed solely to selection logging unless forest stands are alike in all aspects except treatment (i.e. managed versus unmanaged forest stands). For this reason, it was necessary to ensure that all managed and unmanaged forest stands surveyed in 1996 and 1997 had similar physiographies and were subject to similar weather conditions. These aspects of forest stands selected for study could not be determined *a priori*, and were determined in 1996 (for stands A and a through E and e; Figure 1) and in 1997 (for stands F and f through J and j; Figure 1) as follows.

Methods

Physiography

Physiographic data were collected as outlined in the Central Ontario Forest Ecosystem Classification manual (Chambers and Lee 1992). Data for some variables were obtained from available maps. Other physiographic data were collected in each of 5 randomly located 10 x 10 m quadrats per forest stand (Figure 2). In this case, values for each variable collected from each of the 5 quadrats were averaged to obtain one value for each of the

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managed and unmanaged forest stands studied. The elevation (m asl) of each forest stand was estimated from National Topographic Series maps using NAD27 (Table 1). Stand area (ha), mean tree age (y), mean tree height (m) and percent of trees in the stand that were Sugar Maple were determined from Forest Resource Inventory Maps, published in 1994 and available from the Ontario Ministry of Natural Resources. Topographic position, (ranging from 1=top to 5=bottom of slope, 6=depression, and 7=plateau), shape of ground (concave, flat, convex), percent slope (using a SILVA clinometer compass to the nearest percent), length of the upslope and downslope (total slope length is the sum of the upslope and downslope, to the nearest 0.1 m), and aspect (°N) were determined for each quadrat (Chambers and Lee 1992).

Because some of these variables were correlated with each other, I used MANOVA analyses (Manly 1994; Rohlf 1993) to determine whether managed and unmanaged forest stands surveyed in 1996 and 1997 differed significantly from one another with respect to topography (topographic position, percent slope, total slope length, shape of ground) and forest composition (percent Sugar Maple, tree age, tree height). Two-factor ANOVAs were performed to determine whether managed and unmanaged forest stands surveyed in 1996 and 1997 differed with respect to elevation and area. The mean aspect of quadrats in each forest stand was calculated using methods outlined in Zar (1984). A non-parametric, two-sample, second-order analysis of angles, using Watson's two sample test, was used to determine whether the mean aspect of quadrats in managed and unmanaged forest stands surveyed in 1996 and 1997 differed significantly.

Weather

Maximum and minimum air temperatures were recorded to the nearest 0.5 °C, along with a general description of the type and frequency of precipitation, on a daily basis at WRS (Figure 1). Because WRS is equidistant to the three study areas, recorded weather conditions were considered to be representative of all forest stands surveyed over the two

years of the study. Graphs of average weekly maximum and minimum temperatures over time were visually compared to ensure that air temperatures did not differ to any great degree between 1996 and 1997. I used a Wilcoxon signed-rank test (Zar 1984) to compare the average number of rainy days per week in 1996 and 1997.

Results

Physiography of Managed and Unmanaged Forest Stands

Physiographic data collected during summer quadrat surveys were examined to determine whether managed and unmanaged forest stands surveyed in 1996 and 1997 were significantly different from one another. Tests for homogeneity of the variance-covariance matrix for MANOVAs of topography and forest composition data showed that the data were not homoscedastic. Therefore, I used Pillai's Trace as the test statistic, because it is the statistic most robust to heteroscedasticity (Sommers, personal communication).

Forest stands grouped by treatment and survey year did not differ significantly from one another with respect to topography (MANOVA: Pillai's Trace=0.8036; DF_1=12, DF_2=45; P=0.2146) or forest composition (MANOVA: Pillai's Trace=0.8093; DF_1=9, DF_2=48; P=0.0640). Elevation of managed and unmanaged stands (ANOVA: F=1.906; DF=1; P=0.1864) surveyed in 1996 and 1997 (ANOVA: F=0.024; DF=1; P=0.8800) did not differ significantly from one another, and I found no significant interaction between treatment and survey year (ANOVA: F=3.976; DF=1; P=0.0635). The area of managed and unmanaged forest stands (ANOVA: F=1.257; DF=1; P=0.2787) surveyed in 1996 and 1997 (ANOVA: F=0.004; DF=1; P=0.9511) also did not differ significantly. Again, I observed no significant interaction between treatment and survey year (ANOVA: F=0.062; DF=1; P=0.8064). Finally, the mean aspect of quadrats in managed and unmanaged forest stands (Watson's two-sample test: U^2=0.1422; n_1=n_2=10; 0.10<P<0.20) sampled in 1996 and 1997 (Watson's two-sample test: U^2=0.0474; n_1=n_2=10; P>0.50) did not differ

significantly from one another. The mean aspect of all forest stands included in this study was south-southwest 260°, with an angular deviation of 67°.

Weather in 1996 and 1997

Weather conditions were remarkably similar throughout both of the 1996 and 1997 field seasons. There was an average of 2.5 ($\pm$ 1.6 SD) and 2.0 ($\pm$ 1.5 SD) rainy days per week in 1996 and 1997, respectively. A Wilcoxon signed-rank test showed no significant difference in the mean number of rainy days per week of the field season in 1996 and 1997 ($T_-=11$, $T_+=44$; N=11; P=0.0901). Average weekly maximum and minimum air temperatures varied slightly between the two years of the study, but there were no obvious dramatic differences in the temperature profiles of the 1996 or 1997 field seasons (Figure 3).

Discussion

Managed and unmanaged forest stands surveyed in 1996 and 1997 were similar with respect to their physiography and were subject to similar weather conditions. This knowledge, together with knowledge of restrictions used when randomly selecting managed and unmanaged forest stands for inclusion in this study, strongly suggests that observed differences in amphibian habitat, diversity and abundance between managed and unmanaged forest stands surveyed in successive years can be attributed solely to selection logging, since forest stands are alike in all aspects except treatment.

Hairston (1989) emphasizes that knowledge of pretreatment data and the use of proper controls are two of the three absolute requirements of proper experimental design. deMaynadier and Hunter (1995) reiterate this, and state that the absence of these components constitutes one of the major shortcomings of recent studies that have examined relationships between amphibian ecology and timber management. However, they also acknowledge that the absence of accurate pretreatment data for amphibian diversity and

abundance in northeastern forests is due to the almost complete absence of primary, uncut forests able to serve as true experimental controls (Riley and Mohr 1994; Alverson et al. 1994 and Leverett 1993, as cited in deMaynadier and Hunter 1995). Cooperation with forestry companies to time the collection of pre- and post-treatment data with cutting operations is not impossible, but it is very difficult. In many cases, the careful and rigorous matching of a posteriori treatment and control stands, as I have done here, is the only practical solution (deMaynadier and Hunter 1995).

PART II: SPECIES RICHNESS AND HETEROGENEITY

It is difficult to make a priori predictions concerning the diversity of amphibians within contiguous stands of managed and unmanaged forest. On one hand, areas managed for timber production are dissected by an expansive network of logging roads, while unmanaged areas in Algonquin are not. If logging roads prevent migration or dispersal, then it would be appropriate to predict lower amphibian diversity in managed stands. Small, isolated populations are more susceptible to stochastic environmental, genetic, and demographic events, and their risk of decline or extirpation is therefore much greater than that of several larger, non-isolated, adjacent populations (Schaffer 1981; Soulé 1987). Metapopulation (Levins 1970) and island biogeography (MacArthur and Wilson 1963, 1967) theories predict that species diversity will decrease in fragmented habitat due to the higher extinction rates and lower recolonization rates associated with isolated areas.

On the other hand, logging roads could act as dispersal corridors and negate any negative effects of logging on amphibian diversity, or perhaps encourage immigration from other areas. Conflicting evidence exists. Populations of the Common Frog (Rana temporaria) in Germany exhibited lower than average heterozygosity and genetic

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polymorphism, both of which were attributed to population isolation by roads and railways (Reh and Seitz 1990). Conversely, deMaynadier and Hunter (see deMaynadier and Hunter 1995) noted that migrating adults or dispersing juveniles were more likely to cross logging roads than more sedentary individuals moving within established home ranges, and concluded that the effects of logging roads in Maine were probably not strong enough to cause population isolation.

I investigated amphibian species richness and heterogeneity in managed and unmanaged shade-tolerant hardwood forest stands as a crude measure of the effect of timber management on amphibian communities, but I did not make *a priori* predictions about the direction of potential differences in richness or heterogeneity.

Methods

Various survey methods were used to determine the abundance of breeding adults, egg masses and larvae, as well as non-breeding and juvenile amphibians in managed and unmanaged forest stands. These survey methods, chosen for their ability to detect a wide variety of amphibian species at various observable stages in their life cycle, are summarized below (see the Methods sections of Parts III and IV). I pooled information from each of the survey methods to examine and compare species richness and diversity in managed and unmanaged forest stands. Species were recorded as being "present" in a forest stand if they were detected by any one of the survey methods used. I determined the total number of detections for each species present in each forest stand surveyed, by pooling data for breeding adults, non-breeding adults and juveniles detected during surveys of managed and unmanaged ephemeral pools, quadrat surveys and drift fence surveys over both years of the study. I excluded counts of amphibian eggs and larvae from estimates of total abundance because these surveys did not allow me to detect eggs and larvae of all species present, and in the case of Wood Frogs and Spotted Salamanders, egg mass counts and larval estimates were not independent of each other.

I calculated species richness as the number of species detected per hectare in each forest stand, and used a Mann-Whitney U test (Zar 1984) to compare the number of species detected per hectare in both managed and unmanaged forest stands. Because the concept of species heterogeneity (Krebs 1989:329-330) takes both species richness and the abundance of each species into account, I used the Kendall rank correlation coefficient to determine whether there was a significant correlation between the composition of amphibian communities in managed and unmanaged areas (Krebs 1989, Zar 1984).

Results

The average number of species detected per hectare in managed stands (0.44 $\pm$ 0.24 SD) did not differ significantly from the average number of species detected per hectare in unmanaged forest stands (0.28 $\pm$ 0.15 SD). Though unmanaged stands were slightly larger than stands managed under the selection silvicultural system, they did not contain significantly more species of amphibians (Mann-Whitney U test: U=29.5, U'=70.5; $n_1=n_2=10$; P=0.12) (Figure 4).

Analysis of recapture data collected in 1996 showed that recaptures comprised a consistent, but small proportion of the total number of adult and juvenile amphibians caught during surveys of ephemeral pools and drift fence and pitfall trap arrays. However, the comparison of amphibian heterogeneity in managed and unmanaged forest stands sampled in 1996 was not affected by the inclusion of recaptures in calculations of the total number of amphibians detected per species. Recapture data were not collected in 1997, in the interests of time, and because they were not required in repeated measure ANOVA analyses of amphibian abundance (see below, Parts III and IV). Because I couldn't exclude recapture data from both survey years, I pooled the heterogeneity data, including recaptures, for adult and juvenile amphibians collected during all survey methods, in both years of the study, when calculating the total number of amphibians detected per species. I observed a significant, positive correlation between the diversity and abundance of

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amphibians present in communities of managed and unmanaged forest stands (Kendall rank correlation coefficient: Tau=0.79; N=11; P=0.0006), indicating that there is no difference in the heterogeneity of amphibian communities between managed and unmanaged forest stands (Figure 5).

Discussion

Pooling data from all survey methods allowed me to detect 11 of the 12 species of amphibians expected in shade-tolerant hardwood forest habitats of Algonquin (Table 2). None of the survey methods used revealed Two-lined Salamanders (*Eurycea bislineata*). They are likely present in both managed and unmanaged forest stands; however, this species exhibits a close association with forest streams and seepages and my survey methods were not designed to sample these habitats.

Eleven species were found in managed forest stands, whereas only 9 species were found in unmanaged forest stands (Figure 5). It might appear that species richness was slightly, albeit non-significantly, lower in unmanaged forest stands than in managed areas, even when controlling for stand area. However, Gray Treefrogs (*Hyla versicolor*) were heard while conducting surveys of unmanaged forest stands, so the fact that none were observed during amphibian surveys may be due simply to the fact that they did not use the selected ephemeral pools for breeding, or to the fact that they tended to breed in larger, more permanent bodies of water. Bull Frogs (*Rana catesbeiana*) also went undetected in unmanaged forest stands, despite the fact that calls were heard from surrounding forest lakes during nocturnal surveys of ephemeral pools and quadrats. It is entirely possible that Bull Frogs use unmanaged shade-tolerant hardwood forests for dispersal, even though no individuals of this species were detected during surveys of unmanaged forest stands. The only Bull Frogs detected in managed forest stands were a gravid female and a juvenile, both presumably on their respective ways to more suitable habitats. Overall, species

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richness and heterogeneity were extremely similar in managed and unmanaged forest stands.

Estimates of species heterogeneity in managed and unmanaged forest stands could be confounded by the inclusion of recaptures in the abundance data. However, while the estimates of individual species abundances would change slightly, it is highly unlikely that the outcome of the comparison would change. Average recapture rates, as a percentage of the total number of adult and juvenile amphibians captured during surveys of ephemeral pools (managed stands, 2.0 percent; unmanaged stands, 2.3 percent), quadrats (no recaptures), and drift fence and pitfall trap arrays (managed stands, 3.9 percent; unmanaged stands, 1.8 percent), were of similar magnitude in managed and unmanaged forest stands in 1996. As mentioned above, the outcome of comparisons of heterogeneity in managed and unmanaged forest stands surveyed in 1996 did not change with the inclusion or exclusion of recapture data. Because of this, and because others working with amphibian populations in shade-tolerant hardwood forests have observed recapture rates remarkably similar (i.e. 3.9 percent) to those found here (DeGraaf and Rudis 1990), I assumed that recapture rates would be similar for amphibians detected in managed and unmanaged forest stands surveyed in both 1996 and 1997, and therefore assumed that inclusion of 1996 and 1997 recaptures would not affect the outcome of the comparison of heterogeneity in managed and unmanaged forest stands.

That the richness and composition of amphibian communities in managed and unmanaged forest stands is so similar, suggests that selection logging does not fragment hardwood forest habitat to the degree that it interferes with dispersal and colonization rates, even at the stand scale. However, almost no research has been completed on this topic (but see deMaynadier and Hunter 1995), and it is still not conclusively known whether logging roads act as barriers to locally dispersing juveniles and/or migratory breeding adults. Berven and Grudzien (1990) examined the genetic structure of Wood Frog populations in several adjacent breeding ponds in the Appalachians, and showed that populations within a

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1000 m radius of their breeding pond were genetically distinct from other populations near by (as determined by estimates of genetic neighbourhood area and the standardized genetic variance of the populations studied). A small percentage of juveniles would disperse a little more than 1000 m, on average, providing the little existing gene flow between these adjacent populations. I did not recapture any individual amphibian, marked in 1996, in a forest stand other than that in which it was marked. Although this does not prove that there was no immigration or emigration between forest stands surveyed in 1996, it suggests that amphibian movement occurs at or below the stand scale (i.e. over distances of 3 km or less), as found by Berven and Grudzien (1990). In the Martin Lake and Sunday Lake Road areas of Algonquin, logging roads and skidder tracks are pervasive, with roads dissecting every forest stand. It is not uncommon to come across a logging road every 200-500 m along randomly placed transects through managed forests (personal observation). It is quite possible that this degree of habitat fragmentation could isolate populations of amphibians within managed forest stands, and eventually result in lowered species diversity, lowered heterozygosity and lowered frequencies of genetic polymorphisms in these areas, although this remains to be tested.

PART III: AMPHIBIANS AT BREEDING SITES

To my knowledge, nothing is currently known about the effects of partial harvesting on amphibian breeding habitat in upland areas, or of the effects of partial harvests on the abundance and diversity of upland breeding populations of amphibians (but see deMaynadier and Hunter 1995). I reasoned that selection logging would lead to breeding pools of smaller size and shorter duration, as a result of increased incident sunlight and consequent increased water temperatures and evaporation rates, caused by a significant

decrease in canopy cover in managed relative to unmanaged forest stands. I also reasoned that the operation of heavy logging machinery (e.g. skidders) could create new breeding pools and destroy those traditionally used by amphibians, and thus could affect the extent to which ephemeral pools are used by local breeding populations. Together, these effects could reduce amphibian reproductive success and alter the mosaic of source and sink habitats in managed relative to unmanaged forest stands.

Studies of breeding populations of amphibians using ephemeral pools in managed and unmanaged areas corroborate this reasoning. Timber management practices associated with clearcutting in close proximity to a breeding pool result in lower abundance and survivorship of breeding adults (Pechmann et al. 1991; Raymond and Hardy 1991), and reduce anuran abundance by decreasing the duration of breeding pools, which consequently reduces amphibian reproductive success (Enge and Marion 1986). The results of other independent investigations have also shown pool duration to be one of the most important factors regulating adult abundance and juvenile recruitment (Pechmann et al. 1991) as well as larval survivorship (Shoop 1974; Wissinger and Whiteman 1992).

Amphibians exhibit a high degree of breeding site fidelity (e.g. Wood Frogs, Berven and Grudzien 1990; Yellow Spotted Salamanders, Stenhouse 1985), and although breeding individuals will colonize newly created ephemeral pools, colonization requires time. In the Netherlands, where breeding pools were created as part of a conservation effort, pool age was the best predictor of species diversity, and the colonization rate of newly created breeding pools was positively related to amphibian abundance and negatively related to the proximity of forest habitat (Laan and Verboom 1990). If the creation of new breeding pools is accompanied by the destruction of those pools traditionally used by populations of breeding amphibians inhabiting managed forest stands, selection logging could result in a temporary decrease in reproductive success while amphibians find and colonize new breeding sites.

I investigated the effects of selection logging on populations of facultative users of

ephemeral pools at the breeding adult, egg mass and larval stages, in an attempt to determine whether selection logging affects upland populations of breeding amphibians indirectly, by altering reproductive effort and success through the alteration of the availability, size and duration of breeding ponds.

Methods

As the snow was melting in the first week of May of 1996 and 1997, just at the beginning of the breeding season, ephemeral pools were located by walking north-south and east-west transects through each forest stand, listening for calling Wood Frogs and Spring Peepers. I randomly selected one ephemeral pool per stand for sampling, except when only one pool was found. Invariably, managed forest stands were bisected by, or were adjacent to, a logging road and, in these stands only, one of the roadside ephemeral pools was also randomly chosen for sampling. The two types of ephemeral pools in managed forest stands were therefore referred to as "managed" pools and "roadside" pools. Ephemeral pools in unmanaged forest stands were referred to as "unmanaged" pools (Figure 2).

Characteristics of Managed, Roadside and Unmanaged Ephemeral Pools

During the first week of the breeding season, the length and width of each managed, roadside and unmanaged ephemeral pool was measured to the nearest 0.1 m. The surface area of each pool was calculated to the nearest m^2 by using the formula for the area of an ellipse. Maximum depth of each pool was measured to the nearest cm. Later in the summer, percent canopy cover was determined for the center of each pool using a spherical densiometer, as the average of four readings taken to the north, south, east and west. The duration of each pool was determined as the number of days the pool contained standing water, beginning with the first day of the breeding season and ending with the last day in August. An extension of the Kruskal-Wallis test was used to perform non-parametric, two

factor ANOVAs to determine significant differences in the surface area, maximum depth, percent canopy cover and duration of managed, roadside and unmanaged ephemeral pools surveyed in 1996 and 1997. A non-parametric extension of the Tukey test was used for all *a posteriori* multiple comparisons (Zar 1984).

In early May of each year, one maximum-minimum thermometer was placed underwater, in the center of the pool, and water temperatures were recorded to the nearest 0.5 °C on a weekly basis until the end of August, or until the pools dried up. Maximum and minimum temperature data for managed, roadside and unmanaged pools were normally distributed, and raw data were used in simple linear regression analyses that were performed to determine the relationship between maximum and minimum temperature over time for each of the three different pool types. Regressions of pool temperature on time were tested for linearity. Polynomial regressions were fitted to the data when regressions deviated significantly from linearity (Zar 1984). The slope and elevation of linear regressions were compared using methods outlined by Zar (1984) to determine if relationships between pool temperature over time differed significantly between managed, roadside and unmanaged pools.

Abundance of Breeding Adults

For the first five weeks of the breeding season (12 May - 14 June in both 1996 and 1997), nocturnal, time-constrained surveys of ephemeral pools were conducted between 3-5 h after dark, to determine the abundance of breeding adults. Surveyors, 2-4 in number, systematically walked through and around the edges of each ephemeral pool for either 60 or 30 min, respectively. Individual breeding adults of all species encountered were captured. Equal amounts of time were spent in all areas of the pool to capture a representative number of each species present. Special attempts were made to search for silent and inconspicuous species such as Yellow-spotted and Blue-spotted (*Ambystoma laterale*) Salamanders.

In 1996, all captured individuals were taken back to the lab for processing the following morning. One toe from each individual was clipped to indicate the stand in which it had been caught. Toes were stored in labeled eppendorf tubes containing 70 percent formalin. This was done for all species except Red-backed Salamanders, whose toes were too small to clip, in an attempt to determine the recapture rate of adults at breeding sites and movement of individuals between forest stands. All individuals were returned to their point of capture before noon the following morning. In 1997, individuals were processed in the field and returned to their point of capture. Toes were not clipped because examination of the recapture data collected in 1996 suggested that amphibians were not moving between forest stands and because repeated measure ANOVA analyses used to determine differences in the abundance of amphibians between managed and unmanaged forest stands surveyed in 1996 and 1997 (see below, Parts III and IV) did not require the use of recapture data.

Throughout the breeding season, ephemeral pools in managed and unmanaged forest stands were sampled in pairs; during both years of the survey, one pair of managed and unmanaged stands was surveyed per night (Figures 1 and 2). Because nocturnal surveys were conducted 5 nights per week, for the first 5 weeks of the breeding season, each managed, roadside and unmanaged ephemeral pool was sampled once per week, and I could determine a total of 5 repeated measures of breeding adult abundance per pool. I used a three factor (pool type, survey year, week of the breeding season) repeated measure ANOVA (Cody and Smith 1991; Winer 1971) to determine differences in the abundance of breeding adults in managed, roadside and unmanaged pools over the 5 weeks of the breeding season. I also broke these data down and examined differences in the abundance of American Toad, Spring Peeper, Wood Frog and Green Frog (*Rana clamitans*) adults over time for each of the three pool types surveyed in 1996 and 1997. Parametric Tukey tests were used for *a posteriori* multiple comparisons of the repeated measure ANOVA data (Zar 1984).

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Abundance of Egg Masses

Diurnal searches of each managed, roadside and unmanaged ephemeral pool were conducted to determine the total number of Wood Frog and Spotted Salamander (*Ambystoma*) egg masses in each pool. Differences in the number of Wood Frog and Spotted Salamander egg masses detected in each pool type and each year of the survey were determined using an extension of the Kruskal-Wallis test to perform a two-factor, non-parametric ANOVA (Zar 1984).

Abundance of Larvae

Once the egg masses hatched, time-constrained, diurnal surveys were conducted to determine the abundance of amphibian larvae in each pool. Surveys were conducted in the same manner as above: for 30 min, 2 surveyors would systematically walk through and around the entire pool, while using D-nets to capture larvae. Once captured, larvae were contained in buckets filled with water from the pool until they could be identified (Altig and Ireland 1984; Preston 1982), counted, and released at their point of capture after the survey was complete. Larval surveys were conducted at regular intervals throughout the summers of 1996 and 1997 until the ephemeral pools dried up. Although repeated measures of larval abundance were made for each pool sampled in 1996 and 1997, pools were not surveyed with the same frequency in each year because the duration of the various pools fluctuated to a great degree. Therefore, mean numbers of larvae, as well as mean numbers of American Toad, Spring Peeper, Wood Frog, and Green Frog larvae were calculated for each pool. These data were analyzed using an extension of the Kruskal-Wallis test to perform a non-parametric, two-factor ANOVA, to determine whether there were any significant differences in the abundance of larvae between managed, roadside or unmanaged ephemeral pools surveyed in 1996 and 1997 (Zar 1984).

Power Analysis and Variance Partitioning

Using methods described by Cohen (1988), I determined (*a posteriori*) the power of the repeated measure ANOVA to detect a significant difference in the abundance of breeding adults between managed, roadside and unmanaged ephemeral pools. I also determined the sample size necessary to detect a significant difference in the abundance of amphibians in each pool type, at a power of 0.90 and a significance level (alpha value) of 0.10. The proportions of the total variance in breeding adult abundance accounted for by pool type, survey year, week of the breeding season, and the interactions of these factors were estimated for breeding adults by dividing the sums of squares by the total sums of squares for the repeated measure ANOVA model.

Amphibian-Habitat Relationships

I used step-down, stepwise multiple regression techniques (Zar 1984) to determine the nature of relationships between the abundance of breeding adults, egg masses and larvae at breeding sites and the characteristics of managed, roadside and unmanaged ephemeral pools. I used mean numbers of breeding adults, egg masses and larvae per pool in each forest stand, and calculated multiple regressions using data for the surface area, maximum depth, canopy cover and duration of each pool. Multiple regressions were also performed to examine relationships between the abundance of breeding adults and the maximum and minimum temperature profiles of ephemeral pools over time (i.e. week of the breeding season). Prior to proceeding with the multiple regression analysis, I determined whether there were any significant correlations between any of the habitat variables. The correlation matrix of habitat variables was used to interpret multiple regression results.

Results

Characteristics of Managed, Roadside and Unmanaged Ephemeral Pools

Although the surface area of ephemeral pools did not differ between 1996 and 1997 (Kruskal-Wallis: H=1.03; DF=1; 0.25<P<0.50), the surface area of managed, roadside and unmanaged pools differed significantly (Kruskal-Wallis: H=7.46; DF=2; 0.01<P<0.025) (Table 3). Roadside ephemeral pools were significantly smaller than both managed (Tukey test: q=3.45; N=10; P<0.05), and unmanaged ephemeral pools (Tukey test: q=3.23; N=10; P=0.05). Nevertheless, maximum depth did not differ significantly between managed, roadside or unmanaged ephemeral pools (Kruskal-Wallis: H=1.12; DF=2; 0.50<P<0.75) surveyed in either 1996 or 1997 (Kruskal-Wallis: H=2.35; DF=1; 0.10<P<0.25) (Table 3).

There was no significant difference in the percent canopy cover of ephemeral pools sampled in 1996 and 1997 (Kruskal-Wallis: H=2.82; DF=1; 0.05<P<0.10), but the percent canopy cover of managed, roadside and unmanaged pools did differ significantly from one another (Kruskal-Wallis: H=9.77; DF=2; 0.01<P<0.005). Table 3 shows that while the percent canopy cover of roadside pools was significantly lower than the percent canopy cover of unmanaged ephemeral pools (Tukey test: q=4.35; N=10; P<0.05) neither managed and roadside pools (Tukey test: q=1.47; N=10; P>0.05) nor managed and unmanaged pools (Tukey test: q=2.87; N=10; P>0.05) differed significantly from one another with respect to percent canopy cover.

Despite the differences observed in the surface area and canopy cover of managed, roadside and unmanaged ephemeral pools, pool duration did not differ significantly among the three pool types (Kruskal-Wallis: H=0.146; DF=2; 0.90<P<0.95) (Table 3). However, the duration of pools sampled in 1996 (74 days ± 33 SD) was significantly longer than that of pools sampled in 1997 (54 days ± 30 SD) (Kruskal-Wallis: H=4.36; DF=1;

0.025<P<0.05). There was no significant interaction between these two factors (Kruskal-Wallis: H=1.54; DF=2; 0.10<P<0.25).

Maximum and minimum temperature data were normally distributed for all pool types and simple linear regressions were calculated using the raw data. In all cases, regressions of maximum and minimum temperature over time for managed, roadside and unmanaged ephemeral pools yielded significant, positive relationships. The regression of minimum temperature of roadside ephemeral pools over time did not deviate significantly from linearity (Test for linearity: F=6.09; DF=4, 42; 0.10<P<0.25) (Figure 6). However, regressions of minimum temperature over time deviated significantly from linearity for managed ephemeral pools (Test for linearity: F=2.61; DF=4, 41; P<0.0005) and unmanaged ephemeral pools (Test for linearity: F=3.55; DF=4, 30; 0.01<P<0.025). In each of these cases, a third degree polynomial regression was the model that best explained variation in the data (Figure 6). Regressions of maximum temperature over time did not differ significantly from linearity for managed (Test for linearity: F=0.19; DF=4, 40; P>0.25), roadside (Test for linearity: F=0.57; DF=4, 41; P>0.25) or unmanaged (Test for linearity: F=0.44; DF=4, 30; P>0.25) ephemeral pools. Comparisons of regressions of maximum temperature over time for each of the three types of ephemeral pools showed that the regressions did not differ significantly from one another with respect to slope (F=1.29; DF=2, 123; P>0.25) or elevation (F=3.07; DF=2, 125; 0.05<P<0.10). Figure 7 shows the significant, positive relationship between maximum temperature and time common to managed, roadside and unmanaged pools.

Abundance of Breeding Adults

A total of 1527 individual amphibians of 10 species were detected during surveys of managed, roadside and unmanaged ephemeral pools over the 1996 and 1997 field seasons (Table 4). Of these, 1498 (98 percent) were frogs and toads and only 29 (2 percent) were

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salamanders. Together, American Toads, Spring Peepers, Wood Frogs and Green Frogs made up 97 percent of the total number of amphibians detected.

There were no significant differences in the abundance of breeding adults between managed, roadside or unmanaged ephemeral pools (Repeated measure ANOVA: F=0.26; DF=2; P=0.78) sampled in 1996 or 1997 (Repeated measure ANOVA: F=0.77; DF=1; P=0.39). The change in the abundance of breeding adults over the 5 weeks of the breeding season did not differ significantly between any of the pool types (Repeated measure ANOVA: F=1.52; DF=8; P=0.16). The abundance of breeding adults was not consistently higher or lower in either managed, roadside or unmanaged ephemeral pools (Figure 8).

Slightly more Spring Peepers and Wood Frogs were captured in unmanaged ephemeral pools than in either managed or roadside pools (Table 4), but repeated measure ANOVA analyses showed that neither the abundance of Spring Peepers (F=0.41; DF=2; P=0.67) nor the abundance of Wood Frogs (F=1.26; DF=2; P=0.30) differed significantly between managed, roadside or unmanaged ephemeral pools sampled in 1996 or 1997 (Spring Peepers: F=0.04, DF=1, P=0.84; Wood Frogs: F=0.62, DF=1, P=0.44). There was no significant difference in the number of Spring Peepers found among pool types over the 5 weeks of the breeding season (Repeated measure ANOVA: F=0.49; DF=8; P=0.86) (Figure 8). However, the abundance of Wood Frogs observed in managed, roadside and unmanaged ephemeral pools differed significantly over time (Repeated measure ANOVA: F=2.15; DF=8; P=0.04): Wood Frogs were more abundant in unmanaged ephemeral pools early in the breeding season (Figure 8).

Significantly more American Toads were captured in 1997 than in 1996 (Repeated measure ANOVA: F=10.97; DF=1; P=0.003). In addition, the abundance of American Toads differed significantly according to the type of pool surveyed (Repeated measure ANOVA: F=3.19; DF=2; P=0.06). Significantly more American Toads were captured in managed than in unmanaged ephemeral pools consistently over the two years (Tukey test: q=3.45; DF=24; P<0.10); however, the abundance of American Toads did not differ

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significantly between managed versus roadside pools (Tukey test: q=2.53; DF=24; P>0.10) or between roadside versus unmanaged pools (Tukey test: q=0.92; DF=24; P>0.10). Finally, there was no significant difference in the change in the abundance of American Toads over the breeding season (Repeated measure ANOVA: F=1.21; DF=8; P=0.30) for either managed, roadside or unmanaged pool types (Figure 8).

Green Frog abundance did not vary significantly among managed, roadside or unmanaged ephemeral pools (Repeated measure ANOVA: F=1.08; DF=2; P=0.35) sampled in either 1996 or 1997 (Repeated measure ANOVA: F=0.10; DF=1; P=0.75). Neither did the abundance of Green Frogs in managed, roadside or unmanaged ephemeral pools change significantly over the breeding season (Repeated measure ANOVA: F=0.98; DF=8; P=0.45).

A *posteriori* power analysis showed that the power of repeated measure ANOVA tests to detect differences in the mean number of breeding adults in managed, roadside and unmanaged pools was unacceptably low. For an alpha value of 0.10, and an effect size of 0.10, power was equal to 0.16. Approximately 71 of each pool type would be necessary to detect a significant difference in numbers of breeding adults per pool type with alpha and beta both equal to 0.10. My ability to detect changes in the mean number of breeding adults in managed, roadside and unmanaged pools over the breeding season rose to 0.50 with an alpha value of 0.10. In this case, I would only have to increase my sample size to 25 in order to detect a 21 percent difference in the abundance of breeding adults in managed, roadside and unmanaged pools over the 5 weeks of the breeding season (alpha=beta=0.10). Not surprisingly, pool type (1.0 percent), survey year (1.4 percent) and the interaction between pool type and week of the breeding season (4.4 percent) accounted for very little of the observed variance in the mean number of breeding adults. The majority of the variance in breeding adult abundance was accounted for by the error terms in the ANOVA model (variation between individual pools, 44.0 percent; variation associated with individual pools and week of the breeding season, 34.4 percent).

Abundance of Egg Masses

Over the 1996 and 1997 breeding seasons, I observed a total of 476 Wood Frog and 178 Spotted Salamander egg masses in the 10 managed, 10 roadside and 10 unmanaged ephemeral pools sampled (Table 5). Non-parametric, two-factor Kruskal-Wallis tests show that significantly more egg masses were found in 1996 than in 1997 (Wood Frog: H=5.99, DF=1, 0.01<P<0.025; Spotted Salamander: H=5.99, DF=1, 0.01<P<0.025), but the numbers of egg masses did not differ significantly among managed, roadside or unmanaged ephemeral pools (Wood Frog: H=3.84, DF=2, 0.10<P<0.25; Spotted Salamander: H=0.27, DF=2, 0.75<P<0.90).

Abundance of Larval Amphibians

A total of 19,039 individuals of 4 species were detected during larval surveys completed in 1996, and a total of 15,071 individuals of 5 species were detected during larval surveys completed in 1997 (Table 6). The abundance of larvae of all species captured did not differ significantly, either between 1996 and 1997 (Kruskal-Wallis: H=0.95; DF=1; 0.25<P<0.50), or among managed, roadside and unmanaged ephemeral pools over both years combined (Kruskal-Wallis: H=0.51; DF=2; 0.75<P<0.90). Similar results were obtained when data for each species were examined separately. Although significantly more Wood Frog larvae were detected in 1996 than in 1997 (Kruskal-Wallis: H=4.05; DF=1; 0.025<P<0.05), there was no significant difference in the number of American Toad larvae (Kruskal-Wallis: H=0.41; DF=1; 0.50<P<0.75), Spring Peeper larvae (Kruskal-Wallis: H=0.20; DF=1; 0.50<P<0.75) or Green Frog larvae (Kruskal-Wallis: H=1.00; DF=1; 0.25<P<0.50) detected between the two survey years. Neither were there any significant differences in the abundance of American Toad larvae (Kruskal-Wallis: H=4.58; DF=2; 0.10<P<0.25), Spring Peeper larvae (Kruskal-Wallis: H=1.07; DF=2; 0.25<P<0.50), Wood Frog larvae (Kruskal-Wallis: H=0.12; DF=2; 0.90<P<0.95) or Green Frog larvae

(Kruskal-Wallis: H=2.00; DF=2; 0.25<P<0.50) among managed, roadside or unmanaged ephemeral pools.

Amphibian-Habitat Relationships

A step-down, stepwise multiple regression of breeding adult abundance on the surface area, maximum depth, canopy cover and duration of ephemeral pools indicated that only pool duration was significantly related to the abundance of breeding adults. Partial regression coefficients for all other variables were not significantly different from zero. A simple linear regression yielded a significant (F=28.38; DF=1; P=0.0001), positive relationship between the abundance of breeding adults and pool duration for managed, roadside and unmanaged ephemeral pools (y = 0.039 x + 0.129; r^2 = 0.50), and explains approximately 50 percent of the variation in the abundance of breeding adults. The abundance of breeding adults was also positively correlated with both the maximum and minimum temperatures of managed, roadside and unmanaged ephemeral pools (F=5.66, DF=2, P=0.005; y = 0.018 x_1 + 0.034 x_2 + 0.16; r^2 = 0.11). The partial regression coefficient for time was not significantly different from zero.

Similar results were obtained from multiple regression analyses of adult Wood Frog abundance on ephemeral pool variables. Only the partial correlation coefficient for pool duration was significantly different from zero. Simple linear regression analysis yielded a significant (F=16.01; DF=1; P=0.0004), positive relationship between the abundance of Wood Frog adults and the duration of managed, roadside and unmanaged ephemeral pools (y = 0.141 + 0.015 x; r^2 = 0.36) that explained about 36 percent of the variation in the abundance of Wood Frog breeding adults.

This multiple regression analysis was repeated for American Toad and Spring Peeper adults, with slightly different results. American Toad abundance was significantly related only to canopy cover (partial regression coefficients for variables of all other ephemeral pool characteristics were not significantly different from zero). Results of a simple linear

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regression describe a negative relationship between toad abundance and canopy cover of managed, roadside and unmanaged ephemeral pools (F=10.04, DF=1, P=0.004; y = 1.983 - 0.017 x; $r^2 = 0.26$) that accounts for about 26 percent of the variation in toad abundance. Spring Peeper abundance, on the other hand, was simultaneously and significantly, positively related to pool duration and negatively related to canopy cover (F=19.79; DF=2; P=0.0001); together, both variables accounted for approximately 59 percent of the variance in Spring Peeper abundance (y = 0.177 + 0.31 x_1 - 0.011 x_2; $r^2 = 0.59$). Partial regression coefficients for the surface area and depth of managed, roadside and unmanaged ephemeral pools did not differ significantly from zero.

The abundances of both Wood Frog (y = 0.077 x - 1.759; $r^2 = 0.38$) and Spotted Salamander egg masses (y = 0.028 x - 0.349; $r^2 = 0.21$), as well as the abundance of larvae (y = 0.021 x - 0.179; $r^2 = 0.27$), were also positively related to the duration of managed, roadside and unmanaged ephemeral pools. Partial regression coefficients for all other variables were not significantly different from zero. Simple linear regressions of Wood Frog (F=16.92; DF=1; P=0.0003) and Spotted Salamander (F=7.58; DF=1; P=0.01) egg mass abundance on pool duration were significant, and accounted for approximately 38 percent and 21 percent of the variation in egg mass abundance, respectively. A simple linear regression of larval abundance on pool duration was also significant (F=10.50; DF=1; P=0.003) and accounted for about 27 percent of the variation in larval abundance.

Discussion

I did find small differences in the characteristics of roadside pools relative to the characteristics of managed and unmanaged pools. In particular, I found that the positive linear relationship between minimum temperature and time in roadside pools differed from the positive cubic relationship of minimum temperature over time in managed and unmanaged pools, and attributed this difference to the lower canopy cover and smaller size of roadside pools. However, taken in conjunction with the pools' similarity in depth,

duration, and relationship of maximum temperature over time, these differences were not large enough to warrant the general conclusion that selection logging altered the size or duration of ephemeral pools to an extent that one would predict a corresponding difference in the abundance of breeding adults, egg masses or larvae. That the abundance of breeding adult American Toads was higher in managed pools, and the abundance of adult Wood Frogs was higher in unmanaged ephemeral pools early in the breeding season, suggests that selection logging affects ephemeral pool characteristics and breeding populations of amphibians to a degree. However, the lack of difference in the abundance of breeding adults, egg masses and larvae of all other species examined suggests that selection logging does not alter breeding habitat to the degree that it negatively affects the abundance or reproductive effort (i.e. number of egg masses and larvae), of obligate and/or facultative users of ephemeral breeding pools.

Additional support for this conclusion comes from an examination of relationships between amphibian abundance and the characteristics of managed, roadside and unmanaged ephemeral pools. I found that the abundances of breeding adults, egg masses and larvae were significantly and positively related only to pool duration. With the exception of American Toads, whose abundance appeared to be significantly related only to percent canopy cover, this relationship with pool duration held for all species, and explained a notable proportion of the total variance in amphibian abundance at all stages of the life cycle examined. However, the duration of managed, roadside and unmanaged ephemeral pools did not differ significantly from one another, despite the smaller size and lower canopy cover of roadside ephemeral pools, and so variation in the abundance of breeding adults, egg masses and larvae could not be attributed to pool type. Instead, I found that a high proportion of the total variance in amphibian abundance was accounted for by variance among individual pools, and in the interaction of individual pools with time of the breeding season. Together, pool type, survey year and the interaction of pool type with the time of

the breeding season accounted for only 6.8 percent of the total variation in breeding adult abundance.

Unfortunately, the power of the repeated measure ANOVA tests used to detect differences in breeding adult abundance in the three pool types over the course of the breeding season was unacceptably low. My chances of committing a type II error when testing for a pool effect was 84 percent, and 71 pools of each type would have been needed for the respective tests to have sufficient power. However, my chances of committing a type II error when testing for differences in the abundance of breeding adults over the breeding season that were related to pool type were more moderate (i.e. 50 percent). If selection logging were to affect amphibian abundance significantly, then I would expect amphibian abundance to be consistently higher or lower throughout the breeding season in managed versus unmanaged ephemeral pools. This was not the case, suggesting either that there is no effect, as concluded above, or that my sample size was too low to detect small, but real, differences in the abundance of breeding adults, eggs and larvae among managed, roadside and unmanaged ephemeral pools.

Power is a function of effect size (and therefore variability of the data), sample size, and the level of significance. Low effect sizes, a high degree of variation in the data, and low sample sizes will necessarily result in low power (Cohen 1988). Sample sizes required to detect a significant difference in the abundance of breeding adults with equal probabilities of committing type I and type II errors (i.e. alpha and beta both equal 0.10) did not differ by an order of magnitude from those used in this study. Given the low effect sizes, the strong dependence of amphibian abundance on pool duration, and the knowledge that the duration of managed, roadside and unmanaged pools did not differ significantly from one another, I concluded that selection logging does not negatively affect the abundance of breeding adults, egg masses or larvae in managed, roadside or unmanaged ephemeral pools. Nevertheless, further manipulative experiments, using a sufficient number of replicates, would provide a stronger test of this conclusion.

PART IV: AMPHIBIANS IN UPLAND FOREST HABITAT

Evidence suggests that it is the availability of space and suitable moist microhabitats (Fraser 1976; Heatwole 1962; Jaeger 1979; Maiorana 1978), as opposed to the availability of food (Jaeger 1972), that regulates the density and abundance of terrestrial salamanders. The abundance of the American Toad, on the other hand, has been found to be correlated with density of the understory (Pais et al. 1988; Wyman 1988). American Toads are also known for their ability to withstand drier, more urbanized conditions (Conant and Collins 1991; Cook 1984; Tyning 1990). I therefore expected to find fewer Red-backed Salamanders and perhaps more American Toads in managed relative to unmanaged forest stands, because I expected fewer available moist microhabitats in managed forest stands. In particular, I expected to find fewer, larger logs that were moderately to well decayed, and I expected higher soil temperatures, lower soil moistures, decreased leaf litter depth and increased vegetation density in response to lower canopy cover and an increase in the amount of incident radiation hitting the forest floor in managed forest stands.

Quadrat surveys were conducted to assess the abundance of amphibians moving about on the forest floor in the early spring, and drift fence and pitfall trap surveys were conducted in each of the summer, fall and spring seasons to determine whether selection logging changed the timing of amphibian activity on the forest floor in managed relative to unmanaged forest stands. Again, I attempted to determine mechanisms of the effects of selection logging on amphibians by correlating amphibian abundance with specific habitat variables known to be of importance to both Red-backed Salamanders and American Toads, and suspected to be altered in either quality or quantity by the selection logging process.

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Methods

Forest Floor Composition

Five randomly located 10 x 10 m quadrats were established in each forest stand according to methods outlined by Chambers and Lee (1992). One side of each quadrat faced north, and small wooden stakes marked the north east, north west, south east and south west corners of the plot (Figure 2). In July and August, surveys of each quadrat were conducted to characterize the quality and quantity of shade-tolerant hardwood forest habitat available to amphibians. Habitat data were collected in each of the 5 quadrats per forest stand, according to methods outlined in the COFEC manual (Chambers and Lee 1992). Values for each variable collected from each of the 5 quadrats were averaged to obtain one value per managed and unmanaged forest stand.

Within each 10 x 10 m (i.e. 100 m²) quadrat, the area of ground covered by leaf litter, downed woody debris and rock was determined. The area of ground covered by herbaceous vegetation 0-0.5 m in height was also determined, as an index of understory density, or "openness." Leaf litter was collected (down to the humus layer) within a circular, 189 cm² plot just outside one randomly chosen corner of each quadrat. The average number of leaves per 189 cm² plot was used as an index of leaf litter depth in managed and unmanaged forest stands. Canopy cover, estimated from the center of each quadrat, was determined as summarized above for ephemeral pools. These data were analyzed using either a two-factor ANOVA or a non-parametric, two-factor extension of the Kruskal-Wallis test (Zar 1984) to determine whether managed and unmanaged forest stands surveyed in 1996 and 1997 differed significantly from each other with respect to the above characteristics of forest floor habitat.

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Downed Woody Debris

I quantified the downed woody debris available in managed and unmanaged forest stands along two diagonal transects, each 14.4 m long, that ran from the north east to south west and from the north west to south east corners of each quadrat. Each piece of downed woody debris greater than 7.5 cm in diameter, and intersected by one of the transects, was measured and characterized. I recorded the number of pieces of downed woody debris along each transect, as well as the length and diameter of each log, to the nearest 0.1 m and 0.5 cm, respectively. The decay class of each log was also recorded (Table 7), and each log's volume was calculated to the nearest m^3 using the formula for a cylinder. To further characterize the downed woody debris included in the survey, logs were grouped by size class: "pole" logs were between 7.5 cm and 24 cm in diameter; "saw" logs were greater than 24 cm, but less than 50 cm in diameter; and "mature" logs were those greater than 50 cm in diameter. Foresters use this classification to group live trees, except that they define "pole timber" as any tree between 9 cm and 24 cm in diameter (Anderson *et al.* 1990).

Downed woody debris was grouped according to the number of logs (expressed as #pieces/ha) and total volume (expressed as m^3/ha) in each decay and size class, in both managed and unmanaged forest stands surveyed in 1996 and 1997. Differences in the number of pieces, volume, diameter, length, and decay class of downed woody debris in managed and unmanaged forest stands surveyed in 1996 and 1997 were determined using either a two factor ANOVA or two-factor, non-parametric extension of the Kruskal-Wallis test (Zar 1984). Differences in the number of pieces and volume of downed woody debris for each level of treatment (i.e. managed versus unmanaged forest stands), decay class and size class were determined using a three-factor ANOVA (Zar 1984).

Soil Temperature and Moisture

In 1997, soil temperatures were recorded at unique, random locations just a few metres from each drift fence and pitfall trap array (Figure 2) once per week from the second week

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of May through to the second week in August, to the nearest °C using a dial thermometer. Soil samples were taken using a soil corer (25 cm long by 2.5 cm wide), weighed immediately in the field using a portable, battery-operated electronic scale to the nearest 0.1 g, and taken back to the lab for processing. Soil samples were dried in an oven kept at 60 °C until they reached a constant mass. Percent soil moisture was determined by subtracting the final, oven-dry mass of the soil from the sample's initial wet mass, and dividing this amount by the final, oven-dry mass of the soil. Linear regression analyses were used to examine the relationships between soil temperature, moisture and time in managed and unmanaged forest stands. Tests for linearity were performed (Zar 1984) to determine whether regressions were indeed, linear, and polynomial regressions were fitted to the data when regressions deviated significantly from linearity (Zar 1984). The slope and elevation of linear regressions were compared using methods outlined by Zar (1984) to determine if relationships between soil temperature and moisture over time differed significantly between managed and unmanaged forest stands.

Quadrat Surveys

One quadrat per stand, per night was surveyed 2-4 h after dark for the first 5 weeks of the breeding season to determine the abundance of amphibians moving about on the forest floor during the early spring. Rope was tied around the corner stakes to delineate boundaries of the quadrat. Two field assistants started at opposite corners of a quadrat (e.g. north east and south west). With the aid of headlamps, the leaf litter was searched in a thorough, systematic fashion, until all areas of the quadrat had been covered. Leaf litter was searched by hand down to the humus layer (i.e. soil-litter interface). All rocks and logs were rolled over; however, logs were not ripped apart, despite the fact that Red-backed Salamanders could have been inside. Timing was such that habitat surveys to quantify amounts of downed woody debris (summarized above) had to be conducted after the breeding season (i.e. in July - August), and it was therefore necessary to leave downed

woody debris intact. All individual amphibians captured during surveys were processed as summarized above for ephemeral pool surveys in both the 1996 and 1997 field seasons.

Quadrat surveys took between 0.5-1 h to complete, depending on the number of surveyors (2-4) and the amount of litter and woody debris present. Quadrats were surveyed just prior to conducting ephemeral pool surveys for a particular stand. Because a different quadrat was surveyed per stand for each of the 5 weeks of the breeding season (12 May - 14 June in both 1996 and 1997), I could determine a total of 5 independent, repeated measures of amphibian abundance in quadrats of managed and unmanaged forest stands over the breeding season. I used a three factor (stand type, survey year, survey week) repeated measure ANOVA to determine differences in the abundance of all amphibians detected on the forest floor of managed and unmanaged stands over time during the breeding season (Cody and Smith 1991; Winer 1971). I also considered differences in the abundance of Red-backed Salamanders in managed and unmanaged forest stands over time in a separate analysis.

Drift Fence and Pitfall Trap Surveys

One drift fence and pitfall trap array was established at the center of each forest stand and was used to capture juvenile and non-breeding amphibians moving about on the forest floor outside of the breeding season (Figure 2). An array consisted of three arms of landscaping cloth, each 10 m long and supported in a vertical position at regular intervals by wooden stakes. Each arm of the fence stood approximately 80 cm high, and the landscape cloth of each arm of the fence, as well as the supporting stakes, were anchored about 20 cm deep into the ground to prevent amphibians from burrowing under the fence arms. One 2.84 l pitfall trap was placed flush with the ground at the center of each array and at the ends of each arm. Arms of the fence were arranged in a "Y" configuration, with one of each of the arms of the fence pointing in directions of 0, 120 and 240 °N, respectively. The arrays could be opened by turning the cans open side up, and closed by

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turning the cans upside down. When the pitfall traps were open, a synthetic sponge, some leaf litter, and about 2 cm of water were placed in each trap. These features provided shelter and moisture for amphibians.

Arrays were opened for 57 array-nights in the summer of 1996 (23 June - 28 August), 46 array-nights in the fall of 1996 (17 September - 1 November), and for 42 array-nights between 18 May and 7 July in 1997. Once opened, arrays were checked every Monday, Wednesday and Friday before noon. Captured amphibians were processed in the field, as described above for the 1996 and 1997 field seasons. Individuals were released close to their point of capture, several metres away from the array, in order to avoid any immediate recaptures. Both the total number of amphibians and the number of American Toads caught in each array were averaged for each week of the spring, summer and fall seasons. Repeated measure ANOVAs were used to determine differences in the abundance of amphibians and American Toads in managed and unmanaged forest stands in the summer and fall of 1996 and in the spring of 1997 (Cody and Smith 1991; Winer 1971).

Power Analysis and Variance Partitioning

Using methods described by Cohen (1988), I determined (*a posteriori*) the power of each repeated measure ANOVA to detect a significant difference in the abundance of Red-backed Salamanders and American Toads in managed and unmanaged forest stands over time. I also determined the sample size necessary to detect a significant difference in the abundance of Red-backed Salamanders and American Toads in each stand type, at a power level of 0.90 and a 0.10 level of significance (i.e. alpha and beta both equal to 0.10).

The proportion of the total variance in Red-backed Salamander and American Toad abundance accounted for by pool type, survey year, week of the breeding season, and the interactions of these factors were estimated by dividing the sums of squares by the total sums of squares for the repeated measure ANOVA model.

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I used step-down, stepwise multiple regression techniques (Zar 1984) to determine the nature of relationships between the abundance of Red-backed Salamanders, American Toads, and the habitat characteristics of managed and unmanaged forest stands. I used mean numbers of Red-backed Salamanders and American Toads per forest stand, and calculated multiple regressions using averages of the number of leaves in the leaf litter; percent canopy cover; number of pieces, volume, and decay class of downed woody debris; area of ground covered by litter, downed woody debris, and rock; and the area of ground devoid of vegetation, in the 5 quadrats of each managed and unmanaged forest stand. Multiple regressions were also performed to examine relationships between the abundance of Red-backed Salamanders, American Toads, and the profiles of soil temperature and moisture over time (i.e. survey week). Prior to proceeding with the multiple regression analysis, I determined whether there were any significant correlations between the habitat variables. The correlation matrix of habitat variables was used to interpret multiple regression results.

Results

Forest Floor Composition

Significantly less of the ground area in quadrats was covered by leaf litter in 1997 than in 1996 (Kruskal-Wallis: $H=8.69$; $DF=1$; $0.001<P<0.005$). However, there was no significant difference in the area of ground covered by leaf litter between managed and unmanaged forest stands (Kruskal-Wallis: $H=3.16$; $DF=1$; $0.05<P<0.10$), and there was no significant interaction between these two factors (Kruskal-Wallis: $H=0.01$; $DF=1$; $0.95<P<0.97$). Less ground area was covered by downed woody debris in unlogged forest stands (Kruskal-Wallis: $H=4.32$; $DF=1$; $0.025<P<0.05$), but there was no significant difference in the area of ground covered by downed woody debris in quadrats sampled in

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1996 and 1997 (Kruskal-Wallis: H=0.41; DF=1; 0.75<P<0.90) and there was no significant interaction between these two factors (Kruskal-Wallis: H=0.006; DF=1; 0.90<P<0.95). There was no significant difference in the area of ground covered by rock between managed and unmanaged quadrats (Kruskal-Wallis: H=1.60; DF=1; 0.10<P<0.25) sampled in 1996 or 1997 (Kruskal-Wallis: H=0.78; DF=1; 0.25<P<0.50) and there was no significant interaction between these two factors (Kruskal-Wallis: H=2.70; DF=1; P=0.10).

In all cases, deciduous leaves were the dominant component of the leaf litter in both managed and unmanaged forest stands. There were significantly more leaves in the leaf litter of unmanaged forest stands (ANOVA: F=10.32; DF=1; P=0.005), and although fewer leaves were found in the leaf litter of forest stands surveyed in 1997 than in 1996 (ANOVA: F=25.35; DF=1; P=0.0001), there was no significant interaction effect (ANOVA: F=0.40; DF=1; P=0.54). Density of the understory 0-0.5 m tall did not differ significantly between managed and unmanaged forest stands (Kruskal-Wallis: H=0.21; DF=1; 0.50<P<0.75) sampled in either 1996 or 1997 (Kruskal-Wallis: H=2.07; DF=1; 0.10<P<0.25) and there was no significant interaction effect between these two factors (Kruskal-Wallis: H=0.97; DF=1; 0.25<P<0.50).

Canopy cover was significantly lower in managed forest stands (Kruskal-Wallis: H=14.29; DF=1; P<0.001), but there was no difference in the canopy cover of forest stands surveyed in different years (Kruskal-Wallis: H=1.29; DF=1; 0.25<P<0.50) and there was no significant interaction effect between these two factors (Kruskal-Wallis: H=0.02; DF=1; 0.75<P<0.90).

Downed Woody Debris

I found significantly fewer pieces of downed woody debris in unmanaged forest stands (ANOVA: F=11.54; DF=1; P=0.004), despite the fact that there was no significant difference in the volume of downed woody debris between managed and unmanaged forest

stands (Kruskal-Wallis: H=1.65; DF=1; 0.10<P<0.25) sampled in either 1996 or 1997 (Kruskal-Wallis: H=0.28; DF=1; 0.50<P<0.75). In addition, downed woody debris was of a significantly lower mean decay class in managed forest stands (ANOVA: F=7.66; DF=1; P=0.014). Together, this information suggests that there were fewer, but larger pieces of downed woody debris of a higher decay class in unmanaged forest stands. There was no significant difference in the diameter of downed logs in either managed or unmanaged forest stands (Kruskal-Wallis: H=0.63; DF=1; 0.25<P<0.50) surveyed in 1996 and 1997 (Kruskal-Wallis: H=0.01; DF=1; 0.90<P<0.95). However, logs tended to be longer in unmanaged forest stands than in managed forest stands (ANOVA: F=3.15; DF=1; P=0.09).

If logs were indeed fewer but larger in unmanaged forest stands, then further examination of the relationship between the volume and number of pieces of downed woody debris should show either that there were a greater number of the larger saw and mature logs relative to the number of pole logs in unmanaged forest stands, or that the relatively few logs of each size class in unmanaged forest stands were larger and accounted for a greater total volume than did the logs in managed forest stands. Interactions between the number and volume (Figure 9) of logs of each size class did not differ significantly between managed and unmanaged forest stands (number of logs: F=2.02, DF=2, P=0.13; volume of downed woody debris: F=0.02, DF=2, P=0.98); the proportion of pole, saw and mature logs (in both number and volume) were similar in both managed and unmanaged forest stands. However, the discrepancy between the number of pole logs in managed and unmanaged forest stands was greater than the discrepancy between the volume of those logs (Figure 9). This relationship between the number and volume of logs in managed and unmanaged forest stands holds over several size and decay classes (Figure 10), suggesting that there are indeed fewer, larger logs in unmanaged forest stands.

Differences in the number of pieces and mean decay class of downed woody debris in managed and unmanaged forest stands were primarily due to large numbers of pole-sized

logs of decay classes 1 and 2 in managed stands (Figures 9 and 11). When logs in decay classes 1 and 2 were removed from the analysis, there was no difference in the number (ANOVA: F=0.16; DF=1; P=0.69), volume (ANOVA: F=0.80; DF=1; P=0.37), or mean decay class (ANOVA: F=0.17; DF=2; P=0.85) of logs between managed and unmanaged forest stands. In addition, the interactions between the number of pieces of downed wood of each size and decay class in logged and unlogged stands were not significant when downed woody debris of decay classes 1 and 2 was removed from the analysis (Figure 9: F=0.29; DF=2; P=0.75; Figure 10: F=1.45; DF=4; P=0.22). However, the relationships between the volume of downed woody debris of each size and decay class (Figure 9: F=0.40; DF=2; P=0.67; Figure 10: F=3.13; DF=4; P=0.02) did not change with the removal of woody debris in decay classes 1 and 2. With a few exceptions (i.e. saw-sized logs in decay class 5 and mature logs in decay classes 3 and 4), there was generally a higher volume of pole-, saw-, and mature-sized logs in unmanaged forest stands (Figure 10).

Soil Moisture and Temperature

Neither the soil temperature data nor the soil moisture data deviated significantly from normality; therefore, simple linear regressions were performed using the raw data for both variables. There was a significant, positive relationship between soil temperature and time in both managed (F=194.25; DF=1; P=0.0001; r^2=0.74) and unmanaged forest stands (F=197.27; DF=1; P=0.0001; r^2=0.74). The relationship between soil temperature and time in managed forest stands did not differ significantly from linearity (Test for linearity: F=0.18; DF=12, 56; P>0.25), but the same relationship in unmanaged forest stands did (Test for linearity: F=21.37; DF=12, 56; P<0.0005) and was best described by a second degree polynomial, or quadratic model (F=202.11; DF=2, P=0.0001; r^2=0.86). Figure 12 shows relationships between soil temperature and time for managed and unmanaged forest stands.

I found significant, negative relationships between soil moisture and time for both managed (F=7.31; DF=1; P=0.009; r^2=0.10) and unmanaged (F=14.11; DF=1; P=0.0004; r^2=0.17) forest stands. Regressions of soil moisture over time did not differ significantly from linearity for either managed (Test for linearity: F=1.24; DF=12, 56; P>0.25) or unmanaged (F=1.32; DF=12, 56; 0.10<P<0.25) forest stands. The slopes of these regression equations did not differ significantly from one another (t=1.09; DF=136; 0.10<P<0.25), indicating that soil moisture decreased at the same rate over the summer season in both managed and unmanaged forest stands. However, the elevation of the regression of soil moisture over time differed significantly between managed and unmanaged forest stands (t=3.56; DF=133; P<0.001). Soil moisture was slightly, but consistently higher in managed forest stands relative to unmanaged forest stands over the summer season (Figure 13).

Quadrat Surveys

Quadrat surveys completed in 1996 and 1997 revealed a total of 319 individual amphibians of 6 species (Table 8), the majority of which (77 percent) were Red-backed Salamanders. Repeated measure ANOVA analysis shows that there was no significant difference in the abundance of amphibians detected in managed and unmanaged quadrats (F=0.20; DF=1; P=0.66) surveyed in 1996 or 1997 (F=0.001; DF=1; P=0.98). Similar analysis also showed no significant difference in the abundance of Red-backed Salamanders captured in managed and unmanaged forest stands (F=0.37; DF=1; P=0.55) surveyed in 1996 and 1997 (F=0.001; DF=1; P=0.97).

The change in the abundance of amphibians detected in quadrats of managed and unmanaged forest stands over the breeding season differed significantly (F=2.32, DF=4, P=0.07); although amphibian abundance was not consistently higher in unmanaged forest stands over the breeding season, it surpassed the abundance of amphibians found in managed forest stands during the first and last weeks of the breeding season (Figure 14).

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However, the abundance of Red-backed Salamanders did not change significantly between managed and unmanaged forest stands over the breeding season (Figure 14: $F=1.65$; $DF=4$; $P=0.17$).

A *posteriori* power analyses showed that the power of repeated measure ANOVA tests to detect differences in the mean number of Red-backed Salamanders in managed and unmanaged forest stands was unacceptably low. For an alpha value of 0.10, and an effect size of 0.05, power was equal to 0.14. Approximately 344 of each stand type would be necessary to detect a significant difference in the abundance of Red-backed Salamanders with both alpha and beta equal to 0.10. However, I had only a 32 percent chance of committing a type II error when testing for differences in the abundance of Red-backed Salamanders over the 5 weeks of the survey. In this case, I would only have to raise my sample size to 17 in order to detect a 28 percent difference in the abundance of breeding adults in managed, roadside and unmanaged pools over the 5 weeks of the breeding season (alpha and beta both equal 0.10). Not surprisingly, stand type (0.2 percent), survey year (0.001 percent) and the interaction between stand type and week of the survey (7.9 percent) accounted for very little of the observed variance in mean number of Red-backed Salamanders detected in quadrat surveys. The majority of variance was accounted for by the error terms of the ANOVA model (individual forest stands=18.8 percent; the interaction between individual forest stands with survey week=54.8 percent).

Drift Fence and Pitfall Trap Surveys

Drift fence and pitfall trap arrays caught a total of 1,910 amphibians of seven species (Table 9). American Toads comprised the majority of amphibians caught in the summer (97 percent) and fall (54 percent) of 1996, as well as in the spring (91 percent) of 1997, and were consistently more abundant in managed forest stands throughout each of these survey periods. Unfortunately, few individuals of other species were detected (Table 9), making interpretation of data for species other than the American Toad meaningless. Repeated

measure ANOVA analyses were completed for the abundance of all amphibians, and separately for the abundance of American Toads, over each of the seasons surveyed. Because toads comprised such a large proportion of total amphibians caught, results of these two analyses were qualitatively similar and not visibly different from each other when graphed. Therefore, only the results of the analysis of American Toad data are presented below.

There was no significant difference in the abundance of American Toads between managed or unmanaged forest stands in the summer of 1996 (Repeated measure ANOVA: F=1.27; DF=1; P=0.29). However, the abundance of American Toads changed significantly over the course of the summer season (Repeated measure ANOVA: F=2.50; DF=8; P=0.02). Although American Toads were consistently more abundant in managed forest stands, this difference was greatest early in the summer (Figure 15). There were significantly more American Toads in managed forest stands in both the fall of 1996 (Repeated measure ANOVA: F=3.49; DF=1; P=0.10) and the spring of 1997 (Repeated measure ANOVA: F=6.05; DF=1; P=0.04). In addition, the change in the abundance of toads over the breeding season differed significantly for managed and unmanaged forest stands in the fall of 1996 (Repeated measure ANOVA: F=2.38; DF=6; P=0.04) and the spring of 1997 (Repeated measure ANOVA: F=1.97; DF=6; P=0.09). American Toads were more abundant in managed forest stands early in the fall of 1996 and throughout the majority of the spring season in 1997 (Figure 15).

The chances of committing a type II error when testing for differences between the mean number of American Toads caught in drift fence and pitfall trap arrays in managed and unmanaged forest stands were 5 percent ($f=0.26$), 85 percent ($f=0.06$) and 3 percent ($f=0.32$) for the summer 1996, fall 1996 and spring 1997 field seasons, respectively (alpha=0.10). Sample sizes were adequate to detect differences in abundance for both the summer 1996 and spring 1997 field seasons; however, I would have needed to sample 171 managed and unmanaged forest stands in the fall of 1996 in order to detect a significant

difference in the abundance of American Toads in managed and unmanaged stands. A *posteriori* power analyses show that power was equal to 0.64 (f=0.23) , 0.55 (f=0.22) and 0.62 (f=0.24) for tests of differences in American Toad abundance over the summer 1996, fall 1996 and spring 1997 sampling periods in managed and unmanaged forest stands. Sample sizes required to detect a significant effect for the interaction of stand type and survey week were 16 (summer 1996), 23 (fall 1996) and 19 (spring 1997) forest stands, respectively.

Variance in the abundance of American Toads was primarily accounted for by variance due to individual forest stands (summer 1996: 45.7 percent; fall 1996: 14.5 percent; spring 1997: 15.7 percent), seasonal variation in abundance (summer 1996: 24.6 percent; fall 1996: 30.6 percent; spring 1997: 39.1 percent), and the interaction of variance in individual forest stands over time (summer 1996: 17.3 percent; fall 1996: 49.4 percent; spring 1997: 29.0 percent). A very small percentage of the total variance was accounted for by stand type (summer 1996: 6.9 percent; fall 1996: 0.4 percent; spring 1997: 10.3 percent) or the interaction of stand type over time (summer 1996: 5.5 percent; fall 1996: 5.1 percent; spring 1997: 5.9 percent).

Amphibian-Habitat Relationships

Red-backed Salamander abundance was significantly negatively correlated with canopy cover and number of pieces of downed woody debris, and positively correlated with the area of ground covered by leaf litter (F=4.46, DF=3, P=0.02; y = 6.734 - 0.138 x_1 - 0.624 x_2 + 0.124 x_3; r^2 = 0.45). Partial correlation coefficients for all other variables used to characterize forest floor habitat were not significantly different from zero. This multiple correlation accounted for 45 percent of the variation in Red-backed Salamander abundance. Red-backed Salamander abundance was not significantly correlated with either soil temperature or soil moisture over time (F=0.77; DF=3; P=0.52).

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The area of open ground (i.e. ground devoid of vegetation 0-0.5 m high) was the only variable used to characterize the forest floor of shade-tolerant hardwood forest stands that was significantly related to the abundance of American Toads. Partial regression coefficients for all other variables were not significantly different from zero. Simple linear regression analysis yielded a significant, negative relationship between toad abundance and area of open ground (F=7.28, DF=1, P=0.01; y = 1.447 - 0.021 x; r^2 = 0.29). In other words, the abundance of American Toads was positively associated with the density of understory vegetation. The abundance of American Toads was also significantly and positively related to both soil temperature and soil moisture over time (F=15.08, DF=2, P=0.0001; y = 0.124 x_1 + 0.019 x_2 - 0.927; r^2 = 0.31). This multiple regression accounted for about 31 percent of the variation in American Toad abundance.

Discussion

Selection logging did alter managed shade-tolerant hardwood forest habitat in several of the predicted ways. Although there was no difference in the area of ground covered by leaf litter, rock, or understory vegetation between managed and unmanaged stands, I did find that more of the ground area in managed stands was covered by downed woody debris due to the large amounts of slash left by loggers (personal observation). In addition, unmanaged forest stands had significantly more canopy cover and, consequently, there were more leaves in the leaf litter of unmanaged forest stands relative to managed forest stands. A thorough examination of the number of pieces, size and decay classes of downed woody debris suggested that there were fewer, larger pieces of moderately to well decayed downed woody debris in unmanaged, relative to managed forest stands. Finally, and contrary to my initial predictions, relationships between soil moisture and temperature over time were qualitatively different between managed and unmanaged forest stands. While temperature increased linearly over time in managed forest stands, reaching 16 °C by the end of August, it tended to level off at around 14 °C in mid to late July in unmanaged forest

stands. Soil moisture decreased over time at approximately the same rate in managed and unmanaged forest stands; however, soil moisture was consistently higher throughout the summer in managed relative to unmanaged forest stands.

Red-backed Salamanders

Despite finding some quantitative and qualitative differences in hardwood forest habitat in the directions predicted, I did not find a corresponding decrease in the abundance of Red-backed Salamanders in managed forest stands. Although power was not sufficient to preclude committing a type II error when testing for stand effects, it was moderately acceptable for looking at differences in the changes in the abundance of Red-backed Salamanders in managed and unmanaged forest stands over the spring season. Nevertheless, I did not find that Red-backed Salamanders were consistently more or less abundant in managed relative to unmanaged forest stands. Instead, I found that the abundance of Red-backed Salamanders was positively related to the area of ground covered by leaf litter, and negatively related to the number of pieces of downed woody debris, as well as percent canopy cover. Of course, there are two possible reasons for this lack of effect: either selection logging affects shade-tolerant hardwood forest, but not to the degree that it has an effect on the abundance of Red-backed Salamanders; or there is a real difference in Red-backed Salamander abundance, but I could not detect this difference given my methods and sample size.

Results of the multiple regression analysis are initially confusing and thus uninformative when trying to determine a treatment effect. Selection logging decreases canopy cover, but increases the number of pieces of downed woody debris in managed stands. Negative relationships between salamander abundance and each of these variables suggest that Red-backed Salamanders should be more and, at the same time, less abundant in managed forest stands, respectively. The positive relationship between salamander abundance and percent leaf litter cover does not help predict higher or lower abundance of

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Red-backed Salamanders in either managed or unmanaged forest stands, since the area of ground covered by leaf litter did not differ according to stand type.

The confusing nature of the results of this multiple regression cannot adequately be explained by correlations between habitat variables. The correlation matrix for habitat variables suggests that percent canopy cover is positively associated with the decay class of downed woody debris, percent litter cover, and the number of leaves in the leaf litter. These associations make intuitive sense, except that one would expect a positive relationship between salamander abundance, percent leaf litter cover, and percent canopy cover. The number of pieces of downed woody debris is weakly, but negatively correlated with percent canopy cover (suggesting again that there are fewer pieces of downed woody debris in unmanaged forest stands). A strong relationship between salamander abundance and the number of pieces of downed woody debris, as opposed to canopy cover, might force a negative relationship between salamander abundance and canopy cover. I conducted *post hoc*, simple linear regressions to examine the relationships of the abundance of Red-backed Salamanders, canopy cover, and the number of pieces of downed woody debris, but found no significant relationships; nevertheless, the number of pieces of downed woody debris did account for a much higher proportion of the variation in salamander abundance than did percent canopy cover (Red-backed Salamanders and percent canopy cover: $F=4.03^{-5}$, DF=1, P=0.99, $r^2=2.24^{-6}$; Red-backed Salamanders and number of pieces of downed woody debris: F=1.79, DF=1, P=0.20, $r^2=0.09$).

The ambiguous nature of the relationships between these characteristics of hardwood forest habitat and salamander abundance in managed and unmanaged forest stands could be interpreted as evidence for a true lack of effect. Once again, selection logging may alter certain aspects of hardwood forest habitat, but not to the degree that logging negatively affects salamander abundance. Indeed, variance in salamander abundance was primarily due to variation in individual forest stands, night-to-night variation, and variation in individual stands over time. In addition, the abundance of Red-backed Salamanders was

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not related to soil temperature or moisture, despite clear, quantifiable differences in these soil characteristics between managed and unmanaged forest stands. However, it is also possible that my survey methods were not thorough enough to detect subtle differences in salamander abundance that were due to stand type.

The argument for a treatment effect involves the knowledge that salamanders depend on the availability of moist microhabitats, and the prediction that selection logging will cause drier site conditions, with higher soil temperatures, lower soil moistures and fewer, but larger pieces of well decayed downed woody debris. I assumed that Red-backed Salamanders would be equally accessible during surveys of the leaf litter in both managed and unmanaged forest stands. Salamanders are nocturnal, and nocturnal, non-destructive surveys of surface activity have been successfully used by others to examine the abundances of Red-backed Salamanders (Burton and Likens 1975a; Pough et al. 1987). Although it is not known whether surface populations of salamanders are correlated with total population sizes (Test and Bingham 1948), it is generally assumed that surface populations are representative of the total number of salamanders in the area (Hairston 1980, 1986).

This latter assumption may have been unwarranted. Positive associations between terrestrial salamanders and large, moderately to well decayed downed woody debris have been observed by others (Heatwole 1962; Petranka et al. 1994). Assuming that this relationship (as opposed to relationships between salamander abundance and canopy cover or percent leaf litter cover) is most biologically relevant, I should expect to find more Red-backed Salamanders inside the larger, moderately to well decayed logs in the unmanaged forest stands, and fewer salamanders inside the smaller, less well decayed logs of the managed forest stands. If so, then I may have biased my results, because I did not rip logs apart to search for salamanders that may have been inside them. Until more rigorous sampling has been completed, I cannot say conclusively that a treatment effect does not exist. However, the small effect sizes observed, in conjunction with the low proportion of

variance in Red-backed Salamander number that is accounted for by stand type, suggests that selection logging does not affect hardwood forest habitat to the degree that populations of terrestrial salamanders are negatively affected.

American Toads

The abundance of American Toads was positively related to the presence of understory. This relationship has been found by others (Pais *et al.* 1988; Wyman 1988). But given that understory density did not differ significantly between managed and unmanaged forest stands, differences in the abundance of American Toads cannot be attributed to stand type. Other habitat relationships were similarly ambiguous. The abundance of American Toads was positively related to both soil temperature and moisture, but while soil temperature increased as the season progressed, soil moisture decreased over time. These relationships would lead one to predict either higher or lower abundances of American Toads, respectively, later in the season. For these reasons, I suggest that selection logging does not affect the abundance of American Toads by causing changes in understory vegetation density, or changes in the soil temperature and moisture regimes in managed forest stands.

I found more American Toads in managed forest stands than in unmanaged forest stands in both the fall 1996 and spring 1997 surveys using drift fence and pitfall trap arrays. Although a greater proportion of the total variance in American Toad abundance was related to stand type than was the case for any other species or with any other survey method, much of the variance in toad abundance could be attributed to variation within a season and variation between individual forest stands. American Toads were more abundant in managed forest stands early in the summer and later in the spring seasons. In both the summer of 1996 and the spring of 1997, toad abundance was highest in managed forest stands between the end of June through the beginning of July (Figure 15). This is the time when the majority of newly metamorphosed juveniles were seen dispersing over land (personal observation), and by far the majority of toads captured in pitfall traps were

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juveniles, regardless of the season or forest stand. Larval toads were not found to be significantly more abundant in managed forest stands, so differences in toad abundance cannot be attributed to differential reproductive effort. However, higher toad abundance in managed forest stands could plausibly be attributed to higher reproductive success, if more toads survive to metamorphosis in managed forest stands.

GENERAL DISCUSSION

Of the few studies that have examined the effects of timber management on amphibians in upland shade-tolerant hardwood forests of northeastern North America (Ash 1988; Bonin 1991; DeGraaf and Yamasaki 1992; Petranka *et al.* 1993, 1994; Pough *et al.* 1987), all have focused specifically on the responses of terrestrial salamanders and one species of newt in the genera *Plethodon*, *Desmognathus*, *Eurycea* and *Notophthalmus* to clearcutting, (deMaynadier and Hunter 1995). This particular group of amphibians is suspected to be the most sensitive to disturbances that alter the availability and accessibility of moist microhabitats such as downed, decaying logs, leaf litter, and underground root systems. However, other amphibians such as the Yellow-spotted Salamander, American Toad, Spring Peeper and Wood Frog are also common in upland forest areas (DeGraaf and Rudis 1990; Werner 1975), and they, too rely on this habitat for survival and reproduction. This research was conducted in an effort to add to current knowledge of amphibian responses to timber management. With it, I addressed some of the issues emphasized by deMaynadier and Hunter (1995). In particular, I focused on the responses of upland hardwood forest communities of amphibians, and more specifically, the American Toad, Spring Peeper, Wood Frog and Red-backed Salamander, to selection logging, a partial management strategy implemented in the northern hardwood forests of northeastern North America.

Experimental Design

Critiques of biologists' approaches to, as well as conduct and interpretation of ecological experiments are widespread (Drew 1994; Hairston 1989; Hurlbert 1984; Krebs 1991; Peters 1991; Platt 1964). Two of the individual concerns pertinent to studies of amphibian ecology and conservation biology, and relevant to this research, include: (1) interpretation of the results of mensurative versus manipulative experiments, and the lack of pretreatment data for mensurative research (deMaynadier and Hunter 1995; Drew 1994; Krebs 1991); and (2) power and the relative costs of type I versus type II errors (Cohen 1988; deMaynadier and Hunter 1995; Reed and Blaustein 1995; Simberloff 1990). I discuss these issues as they relate specifically to this research in the spirits of Toft (1990), Simberloff (1990), and Cohen (1988), who acknowledge that statistics is but one of the tools used by ecologists to interpret results of ecological experiments and evaluate the "Truth" of scientific hypotheses.

Comparative Mensurative Experiments

By far the majority of studies investigating the effects of timber management at the organism or ecosystem level are forced to use comparative mensurative experiments, as defined by Hurlbert (1984) (e.g. this study, Petranka et al. 1993, 1994; Pough et al. 1987; but see Schmiegelow and Hannon 1993; Schmiegelow et al. 1997). The seemingly obligatory nature of the mensurative, as opposed to the manipulative approach, results primarily from the lack of virgin, uncut forests to use as true controls (deMaynadier and Hunter 1995; Riley and Mohr 1994), in conjunction with the difficulty of arranging cooperation between researchers and timber management organizations on the necessary spatial (e.g. number and size of replicates and controls) and temporal (e.g. the relatively short duration of graduate degrees and/or funding agreements) scales (deMaynadier and Hunter 1995). Perhaps the most important shortcoming of this approach concerns biologists' inability to determine conclusively, and to the exclusion of all possible alternate

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hypotheses, that observed differences are due to a treatment effect; that is, that logging and not some other preexisting environmental gradient or chance event (Hurlbert 1984) significantly, positively or negatively, affects the organism or system under study (Drew 1994, Platt 1964).

In the specific case of the investigation of the effects of timber management on amphibians, the only practical solution offered by deMaynadier and Hunter (1995) involves the rigorous matching of control (i.e. second growth forests) and treatment (i.e. logged) study sites. Extensive knowledge of "pretreatment" conditions; that is, that control and study sites are alike in all aspects (e.g. climate, elevation, topography, floral and faunal community compositions) except treatment (i.e. logged versus unlogged), should enable researchers to determine, based on results of their comparative mensurative experiments, whether or not it is the treatment that is responsible for observed differences in the abundance of the species or assemblage of amphibians in question. However, no two sites are ever exactly the same, nor can they be expected to remain identical prior to, during, and after the mensurative experiment has been completed (Hairston 1989; Hurlbert 1984). Therein lies the rub. Correlation does not imply causation, but correlation is the only thing that comparative mensurative experiments can demonstrate, and a comparative mensurative experimental design is often the only option.

The true problem here is one of unsubstantiated confidence in the results of a mensurative experiment, and the use of those results to make conclusive, causative statements about treatment effects. I have demonstrated above that the managed and unmanaged stands used in this study are alike in many aspects; namely, disturbance history prior to the implementation of selection logging in managed stands, physiography, climate and forest composition. I use this information to suggest that observed differences in amphibian habitat, diversity and abundance can only be the result of selection logging. I realize, however, that it should be the priority of future research to conduct manipulative experiments to validate these results (to the extent possible; see Hairston 1989), as well as

to determine the mechanisms responsible for the observed differences in amphibian habitat and abundance between managed and unmanaged shade-tolerant hardwood forest stands.

Power Analysis

The potential of power analysis in scientific research of many, and perhaps all disciplines has long been ignored. Instead, emphasis has been placed on the statistical significance (i.e. alpha, or probability of committing a type I error) of the result and away from the size of the effect being pursued (Cohen 1988). The effect of this emphasis has been to elevate the status of the 0.05 alpha level of significance from a useful, informative convention to a blindly accepted, absolute criterion, and to confuse the importance of detecting type I versus type II errors (Cohen 1988; Simberloff 1990; Toft 1990). Recently, the relative costs of these two types of statistical errors have been the subject of much discussion, especially in conservation biology, where the costs of failing to reject a false null hypothesis (type II error) often far outweigh the costs of rejecting a true null hypothesis (type I error) (deMaynadier and Hunter 1995; Taylor and Gerrodette 1993).

Power, the complement of beta (i.e. the probability of committing a type II error), is the probability that a statistical test will yield significant results (Cohen 1988). Results of literature surveys show that power in some fields, such as abnormal psychology, ranges from 37-50 percent at the 0.05 level of significance (Cohen 1988). This record is no better for studies of amphibian ecology, in which power has been found to range from 6-45 percent at the 0.05 level of significance (Reed and Blaustein 1995). All things being equal, this means that researchers are implicitly accepting the fact that they have between a one in twenty to a one in two chance of detecting a significant difference if, indeed there is one, and that the probability of failing to reject a false null hypothesis ranges from 50-94 percent.

Conventionally, "failure to find" is less serious an error than "finding something that's not there" (Cohen 1988) and researchers have rightly focused their attention on minimizing

alpha. However, this convention can be dangerous when the results of research are used to make management recommendations or policy decisions (Taylor and Gerrodette 1993). The results of my investigation of the effects of selection logging on amphibian diversity and abundance could very easily be used to recommend the maintenance of currently implemented selection logging protocol. From an ecological viewpoint, the cost of not finding a (negative) effect when there actually is one is quite high, if it results in the loss of amphibian diversity and/or the local extinction of amphibian populations throughout Algonquin Park and other shade-tolerant hardwood areas managed using selection logging (cf. Petranka *et al.* 1993). But from an economic viewpoint, the cost of finding an (negative) effect when it doesn't exist is high if this results in lower quotas, increased rotation time, or otherwise decreases the amount of money gained from timber harvest. In this case, it could be argued that type I and type II errors are at least equally costly from both economic and ecological viewpoints (see Simberloff 1990), and beta should be minimized at the expense of small increases in alpha (Cohen 1988; deMaynadier and Hunter 1995; Schmiegelow *et al.* 1997; Welsh and Lind 1995).

Power can be increased by increasing sample size, decreasing the variability of the data, increasing alpha, and/or increasing the desired effect size. Sample size, alpha and beta should be set by the researcher *a priori*, with an understanding of the effect size one wishes to detect, and the relative costs of type I versus type II errors (Cohen 1988). Usually, knowledge of effect sizes are based on estimates made from the literature, and required sample sizes can be determined for set values of alpha and beta. Because no previous studies had been completed on the effects of partial harvests on amphibians, it was impossible to estimate the effect size, f, and I assumed that the effect size would be much lower for selection logging than for clearcutting. In an attempt to increase the power of my tests and decrease beta, I used as large a sample size as was practically possible, used repeated measures of amphibian abundance in an attempt to decrease the variability of these measures, and used a moderate alpha value of 0.10. Despite these attempts, my chances of

committing a type II error were often unacceptably high, even at the 0.10 significance level. However, if low power is primarily the result of low effect sizes (i.e. effect sizes approximately equal to or less than 0.10) and the required sample size does not differ greatly (i.e. by an order of magnitude) from the one used, it can be assumed that, for all practical purposes, there is no treatment effect. I have formulated the following discussion of the results of my research with this in mind.

Hardwood Forest Habitat

Results of this research suggest that selection logging does affect shade-tolerant hardwood forest habitat in two important ways. First, slash piles consisting of the crowns and other small branches of trees left by logging cover a greater area of ground in managed forest stands than downed woody debris (either single logs or whole windblown trees) in unmanaged forest stands. The high number of pole logs in decay classes 1 and 2 accounted for many anomalies observed in the comparisons of the average decay class, number of pieces and average volume of downed woody debris between managed and unmanaged forest stands. Removal of these logs from the analysis allowed a clearer comparison of the differences in the availability of downed woody debris in decay classes 3 to 5 within managed and unmanaged forest stands; that is, a comparison of the types of downed woody debris most often used by amphibians for refuge, foraging and/or reproduction (Heatwole 1962; Petranka et al. 1994). I found that there was no significant difference in the number of pieces, mean decay class, or volume of downed woody debris between managed and unmanaged forest stands. However, examination of the interaction of stand type, decay class and size class revealed that overall, there was a greater volume of downed woody debris of decay classes 3 to 5 in unmanaged stands than in managed forest stands. Further comparisons showed that discrepancies between the two stand types in the number of pieces and volume of downed woody debris in a given size and decay class were often

large; there tended to be fewer, larger pieces of downed woody debris in unmanaged forest stands.

Second, selection logging decreases canopy cover by 14 percent in managed forest stands through the removal of saw logs (Enright, unpublished data). Reduction in the canopy causes a reduction in the number of leaves in the leaf litter, but does not affect the area of ground covered by leaf litter. The density of understory vegetation is also not affected, despite the increased availability of light and nutrients (Likens et al. 1978). However, reduction in the number of saw logs reduces transpiration in managed stands and causes significant differences in the soil temperature and moisture regimes of managed and unmanaged forest stands. Notably, the relationship of soil temperature over time is linear in managed stands, but quadratic in unmanaged forest stands. Where soil temperature in unmanaged stands begins to level off at about 14 °C in mid July, it continues to increase to above 16 °C through late August in managed forest stands. Soil moisture is consistently higher from May through August in managed forest stands relative to that in unmanaged forest stands, although soil moisture decreases at the same rate in both stand types over the summer season. Likens et al. (1978) observed a similar phenomenon in clearcut hardwood forests. During the summer, reduced transpiration causes the upper few centimetres of soil in an experimentally deforested system to be very dry while the lower layers are very moist. In a forested ecosystem, however, the humus layer is moist, and transpiration keeps the deeper mineral layer relatively dry.

Selection logging does not appear to alter the number, size or duration of ephemeral breeding pools in managed forest stands. Roadside pools are generally smaller than either managed or unmanaged ephemeral pools, but unexpectedly, they do not differ from either managed or unmanaged pools in duration or maximum depth. Canopy cover is reduced over roadside pools relative to unmanaged pools, but the relationship of maximum pool temperature with time is identical for each pool type. Managed and unmanaged ephemeral pools, on the other hand, appear identical in all respects I examined. Whereas the

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relationship of minimum pool temperature over time is linear in roadside ephemeral pools, it is a cubic relationship in both managed and unmanaged ephemeral pools over the spring and summer seasons.

Comparisons of the above attributes of hardwood forest habitat were made 2-3 years after forest stands had been logged, and a minimum of 40-50 (but most likely as great as 60) years after disturbance for unmanaged habitat. What is not clear at this point, is the time necessary for canopy cover, soil moisture, leaf litter, and downed woody debris in partially harvested shade-tolerant hardwood forest stands to "recover" to those levels of unmanaged stands. Stands managed under selection logging are managed on a 20 to 30 year rotation. As such, the managed forest stands included in this study have been logged at least twice. Recovery periods longer than 20 years may mean that hardwood forest habitat in logged stands will continue to degrade over time. On the other hand, recovery periods less than 20 years mean that the selection logging process is truly sustainable, as far as can be determined.

The relationships between a stand's management age, rotation time and habitat "quality" are important. Short rotation times have a much greater effect on the composition and dynamics of the forest floor microhabitat than does harvesting intensity (Aber et al. 1978). Amphibians, especially terrestrial salamanders, rely upon the aspects of shade-tolerant hardwood forest habitat that differed significantly between managed and unmanaged forest stands. But with the exception of American Toads, I found no significant differences in the diversity or abundance of amphibians between managed and unmanaged forest stands at any stage in their life cycle, suggesting that selection logging does not alter hardwood forest habitat to the degree that this type of silviculture negatively affects amphibian diversity and abundance. This could change with time, however, if logging continues to degrade those aspects of forest habitat on which amphibians depend. Bormann and Likens (1979, as cited in Hughes and Fahey 1994) suggest that northern hardwood forest stands disturbed by hurricanes or forest harvest recover after approximately 30 years, the rotation

period typical of stands managed under selection logging. But others have found that habitat characteristics of known importance to amphibians continue to recover for periods of 50-80 years, and perhaps longer (Aber et al. 1978; Covington 1981). For example, leaf mass production (Hughes and Fahey 1994) and the thickness of the forest floor (Federer 1984) increase with increasing stand age. The organic matter content of the forest floor reaches levels of mature forest stands only after approximately 50 years of recovery (Federer 1984).

Amphibian Diversity and Abundance

Petranka et al. (1993, 1994) have provided the only estimates of amphibian diversity in clearcut hardwood forests of eastern North America. They found that the diversity of salamanders within the genera *Plethodon* and *Desmognathus* was significantly lower in clearcut than in recently undisturbed hardwood forests of the southern Appalachians at both high and low elevations, respectively. Diversity increased with increasing age of the stands sampled, and reached a maximum in stands 50-70 years old at high elevations (Petranka et al. 1993), and a maximum in stands 120-200 years old at lower elevations (Petranka et al. 1994). No old growth (i.e. virgin) forests were included in their studies, so it is unknown whether diversity would continue to increase with forests older than those included in either of their studies. A similar phenomenon has been observed for the abundance of amphibian populations in northern hardwood forests. Bonin (1991), Petranka et al. (1993, 1994), and Pough et al. (1987) suggest that amphibian populations recover from clearcutting in northern hardwood forests that have reached ages of 30-60, 60-120, and 60 years, respectively.

Some have advanced the hypothesis that it is not the age of forest stands themselves that is positively correlated with amphibian abundance and diversity, but the microhabitats associated with older forests (Welsh 1990). The coincidence of amphibian population recovery with the functional recovery of northern hardwood forest microhabitats around the

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60 year mark (Aber *et al.* 1978; Covington 1981; Federer 1984) seems to lend support to this hypothesis. Work by Petranka *et al.* (1994) that relates the recovery of terrestrial salamanders to the recovery of large pieces of downed woody debris that are moderately to well decayed also supports this line of reasoning. It seems plausible, then, that selection logging, which maintains some structural integrity of hardwood forest stands, and maintains them at about an age of 150 years, might have negligible effects on amphibian diversity and abundance.

American Toads were significantly more abundant in managed forest stands, both as breeding adults and as dispersing juveniles caught in drift fence and pitfall trap surveys. But aside from differences in toad abundance, I could find no differences in the diversity or abundance of breeding adults, egg masses or larval amphibians, either as a group or on a species-by-species basis, in managed versus unmanaged forest stands. Results of amphibian-habitat relationship analyses suggest that selection logging does not affect shade-tolerant hardwood forest habitat to the degree that observed differences in habitat "quality" causally affect amphibian abundance. Although power was often low, I concluded that the low effect sizes, and the low proportion of variance accounted for by stand or pool type precluded the conclusion that selection logging affects amphibian diversity and abundance. Even though this conclusion may be warranted, there remains the possibility of a type II error; that is, the wrongful conclusion of no effect.

The costs and benefits of conducting mensurative versus manipulative experiments on a scale as large as this have been discussed. But just because such a large scale manipulative experiment is absolutely not feasible in many cases, does not mean that other avenues of investigation do not exist. I investigated the effects of selection logging on the diversity and abundance of amphibians, assuming that any negative effects of selection logging on hardwood forest habitat would, in effect, create "sink" habitats for amphibians, and that this would translate directly into lowered amphibian abundance. However, it is theoretically possible for sink habitats to support large populations of organisms (Pulliam 1988). If

there is active dispersal from nearby source habitats, where the availability of high quality breeding habitat is limited, but fitness is high, then surplus individuals that actively select suitable habitats (e.g. juveniles or less competitive individuals) must go elsewhere to breed. Continuous replenishing of sink habitats with surplus individuals from source habitats can maintain sink populations of individuals, in which birth rates (i.e. reproductive success) are lower than mortality rates (Pulliam 1988).

Selection logging may create sink habitat, and the nearby unmanaged forest stands (or forest stands nearing the end of their rotation cycle), source habitat. In this case, selection logging may not appear to affect the abundance of amphibians in managed forest stands. Further research is needed to investigate amphibian movements both between and within managed and unmanaged forest stands and to determine whether timber management protocols associated with partial harvests such as selection logging affect the reproductive success of terrestrial amphibians, as well as facultative or obligate users of ephemeral breeding pools and permanent ponds. This research should ideally take the form of a manipulative experiment, and results of power analyses conducted here should be used when estimating *a priori* effect sizes and setting sample sizes, and alpha and beta.

Management Considerations

Studies of the effects of clearcutting on amphibian diversity and abundance in both deciduous and coniferous forests have found that this type of timber harvest negatively affects amphibian populations (deMaynadier and Hunter 1995). Researchers have attributed differences in diversity, abundance, and/or survivorship solely to logging itself (Raymond and Hardy 1991), but usually also attempt to determine some mechanism behind these declines with the hopes of making constructive recommendations for forest management plans, or timber harvest protocols. For example, Petranka *et al.* (1993, 1994) examine the relationship of stand age and amphibian diversity and abundance. Upon finding that terrestrial salamander populations appear to recover between 60-120 years after

clearcutting, they recommend longer rotation cycles, the establishment of old-growth forest reserves (i.e. no cut zones), maintenance of buffer zones around headwater streams and seepages, and the use of innovative harvest methods that leave the basic structure of the forest intact (Petranka et al. 1994). Pough et al. (1987) examine the effects of various harvesting protocols on Red-backed Salamanders and Eastern Red-spotted Newts and also recommend, at a minimum, the maintenance of significant, representative areas of forest from all forms of disturbance, so that habitat is preserved for those species that depend upon old-growth forest for survival. Similarly, Welsh and Lind (1995) recommend the protection of buffer strips around all aquatic habitats, as well as the maintenance of a sufficient number of forested areas with appropriate microhabitats between drainages to allow for gene flow and the repopulation of Del Norte Salamanders into harvested areas. As a final example, Dupuis et al. (1995) recommend that foresters maintain an even distribution of logs and snags as stable, moist microhabitats, retain some understory as a source of shade, preserve streamside buffers and ensure some degree of landscape connectivity to enable climate-sensitive species to disperse and recolonize marginal habitats.

Although the above recommendations are not wrong, they are not as practically useful as they could be. Management recommendations must be quantified before they can be implemented. For example: how long should rotation cycles be; how wide should buffer strips be; should many small, or a few large old-growth forest fragments be maintained as no-cut zones; are the basic structural components of a forest necessarily equally important to all major groups of terrestrial vertebrates; and what size and density of downed logs are necessary to provide sufficient habitat for salamanders in clearcut forests, if this is at all possible? In order to effectively, efficiently exploit timber as a renewable resource, we must come to a mechanistic understanding of how all methods of timber harvest affect forest habitat, what natural recovery mechanisms exist within particular forest types, and at what rates they occur (Likens et al. 1978). In addition, we must be able to quantify and conclusively demonstrate cause and effect relationships between timber management

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strategies used in all forest types and their effects on various wildlife species, using the results of strong inference and manipulative experiments (Hurlbert 1984, Platt 1964). Until we have achieved this degree of mechanistic understanding, even the most constructively made recommendations will not be specific enough, or convincing enough, to be implemented by foresters. Although the focus of government and forestry companies may slowly be changing to incorporate ecological interests more and more often, decisions involving changes to timber harvesting protocols are made primarily on an economic basis. If biologists aspire to influence constructive changes to timber management protocols, then we must quantify these changes based on scientifically sound evidence of cause and effect. We must be able to convince governments and forestry companies that the cut in short-term economic gains means the increase in long-term investments in a renewable resource.

I have concluded that I cannot detect negative effects of selection logging on the diversity or abundance of amphibians inhabiting the shade-tolerant hardwood forests of north eastern North America. This conclusion does not, as yet, warrant the unqualified endorsement of selection logging as a sustainable timber management strategy, but it also does not warrant the proposition of any constructive changes to selection logging protocol as it is currently implemented in northern hardwood forests. A good deal of research must be completed in order to validate these results, before any management recommendations can be made in a useful, quantifiable and definitive manner. First of all, an investigation of the effects of selection logging on Red-backed Salamander populations should be repeated in an unbiased manner according to recommendations made above, in order to determine conclusively whether selection logging affects Red-backed Salamanders in a negative way. In addition, future research should focus on the investigation of managed and unmanaged forests as either source or sink habitats for amphibians according to Pulliam's (1988) model. By investigating movements of immigrating and emigrating amphibians (especially dispersing juvenile American Toads) between managed and unmanaged areas, as well as the reproductive success of those individuals inhabiting managed and unmanaged forest

stands more effectively than could be done here, knowledge of whether and how selection logging affects amphibian populations should become evident, and facilitate constructive recommendations for the maintenance of, or changes to currently implemented selection logging practices.

SUMMARY

Despite amphibians' widely acknowledged importance in terrestrial forest ecosystems, they are rarely included in forest management plans. The impact on these organisms by forest management activities is rarely acknowledged, or even considered, in part because very little is known about the effects of, or amphibian response to, timber management. Recent studies show that clearcutting in both deciduous and coniferous forests results in lowered amphibian diversity, abundance and survivorship, but to date, no studies have been completed on the effects of partial harvests. In order to determine whether, and if so, by what mechanism, selection logging affects amphibians in shade-tolerant hardwood forests, I compared amphibian habitat concurrently with amphibian diversity and abundance in logged and unlogged forest stands in Algonquin Provincial Park, Ontario.

Selection logging significantly altered aspects of shade-tolerant hardwood forest habitat on which amphibians are known to depend. Among other things, logging decreased the number of leaves in the leaf litter; resulted in fewer, larger, moderately to well decayed pieces of downed woody debris; and significantly altered soil moisture and temperature relationships in managed relative to unmanaged forest stands. However, with the exception of American Toads, that were consistently more abundant in managed forest stands, the diversity and abundance of amphibians (in particular, adult Red-backed Salamanders and all observable life stages of Spring Peepers, Wood Frogs and Green Frogs) did not differ

significantly between managed and unmanaged areas. Power was not always high enough to avoid committing a type II error; but, given the low effect sizes, and that variance in amphibian abundance was primarily accounted for by variation in individual forest stands or ephemeral pools and variance in individual forest stands over time, I concluded that selection logging did not alter hardwood forest habitat to the degree that it significantly affected amphibian diversity or abundance.

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Table 1. Characteristics of forest stands under study. Those stand numbers with prefixes SLR-, MLR- or H60- are located in the Sunday Lake Road, Martin Lake Road and Highway 60 corridor areas of Algonquin Provincial Park, respectively. SLR and MLR sites were logged in 1993-1994 and 1994-1995, respectively. H60 forest stands have been left undisturbed for at least 40-50 years.

Stand Number[1]	Year Surveyed	UTM (NAD27)[2]	Elevation (m asl)	Stand Area (ha)	Mean Tree Age (y)	Mean Tree Height (m)	Tree Species Composition[3]
SLR-1453 (A)	1996	70143-505535	472	12	156	21.7	Mh7, Be1, By1, He1
SLR-1844 (B)	1996	70200-505437	503	13	131	21.8	Mh8, By1, He1
SLR-2852 (C)	1996	70290-505530	488	11	120	25.4	Mh8, Be2
SLR-2737 (D)	1996	70280-505385	472	19	131	21.8	Mh7, Be1, He2
SLR-3943 (E)	1996	70394-505428	472	43	131	21.8	Mh7, Be1, By1, B1
MLR-3157 (F)	1997	69311-503581	503	8	121	20.4	Mh9, He1
MLR-0559 (G)	1997	69052-503591	488	26	136	20.3	Mh7, Be1, By1, Pw1
MLR-2287 (H)	1997	69223-503877	518	31	136	20.3	Mh6, Be2, By1, B1
MLR-3489 (I)	1997	69335-503896	488	26	131	20.3	Mh10
MLR-2689 (J)	1997	69263-503890	518	17	136	20.3	Mh8, By1, B1
H60-2193 (e)	1996	69217-504938	488	16	173	21.0	Mh8, Be2
H60-1391 (d)	1996	69138-504905	472	57	146	20.2	Mh6, Be2, By1, He1
(c)	1996	69039-504097	503	16	146	20.2	Mh8, Be1, Ms1
H60-9684 (b)	1996	68968-504837	488	12	139	19.1	Mh9, Be1
H60-9674 (a)	1996	68962-504741	488	41	146	21.7	Mh6, Be1, By1, Ms1, He1
H60-6701 (f)	1997	68675-505024	503	43	151	21.7	Mh9, By1
H60-6788 (g)	1997	68670-504885	518	29	146	20.2	Mh7, Be1, By1, He1
H60-8769 (h)	1997	68880-504718	442	25	131	21.8	Mh7, Be1, By2
H60-7079 (i)	1997	68695-504785	442	32	131	20.3	Mh6, By3. He1
H60-8174 (j)	1997	68815-504740	442	7	151	20.2	Mh9, By1

[1] Data in this table are taken from Ontario Forest Resource Inventory (FRI) Maps published in 1994 by the Ontario Ministry of Natural Resources.

[2] UTM stands for the "Universal Transverse Mercator" grid used on FRI maps and National Topographic System (NTS) maps. UTMs are given to the nearest ten metres. NTS Maps used to determine UTM coordinates used North American Datum 1927.

[3] Notation used by OMNR to describe tree species composition in forest stands. Mh7, for example, simply means that 70% of the trees in a particular forest stand are Sugar (Hard) Maple. (B=Balsam Fir; Be=American Beech; Bw=White Birch; By=Yellow Birch; He=Eastern Hemlock; Mh=Sugar (Hard) Maple; Ms=Red (Soft) Maple; Pw=White Pine)

Table 2. A list of amphibian species known from Algonquin Provincial Park, Ontario (after Strickland and Rutter 1992). Those species expected to be detected during amphibian surveys of shade-tolerant hardwood forest habitat in the west side of the Park are indicated.

Scientific Name	Common Name	Habitat	Expected in Surveys
Necturus maculosus	Mudpuppy	lakes, rivers, streams	
Notophthalmus viridescens	Red-spotted Newt	efts: forest leaf litter adults: lakes, streams	yes
Ambystoma laterale	Blue-spotted Salamander	forest litter, lakes, ponds	yes
Ambystoma maculatum	Yellow-spotted Salamander	forest litter, lakes, ponds	yes
Eurycea bislineata	Northern Two-lined Salamander	forest streams, litter	yes
Plethodon cinereus	Redback Salamander	forest leaf litter, logs	yes
Bufo americanus	Eastern American Toad	forests, meadows, urban	yes
Hyla versicolor	Gray Treefrog	wet forest or scrub	yes
Pseudacris triseriata	Western Chorus Frog	forests, meadows, urban	
Pseudacris crucifer	Northern Spring Peeper	forest litter, ponds, swamps, wet scrub	yes
Rana sylvatica	Wood Frog	moist forest litter, lakes	yes
Rana pipiens	Northern Leopard Frog	moist meadow areas	
Rana palustrus	Pickerel Frog	sphagnum bogs, meadow streams	
Rana clamitans	Green Frog	forest/urban lakes, ponds	yes
Rana septentrionalis	Mink Frog	lakes, ponds, streams	yes
Rana catesbeiana	Bull Frog	lakes, swamps, bogs	yes

Table 3. Characteristics of 10 managed, 10 roadside, and 10 unmanaged ephemeral pools surveyed in 1996 and 1997 in Algonquin Provincial Park, Ontario. Means (± SD) designated with the same letter do not differ significantly from one another at the 0.05 level of significance.

Pool Type	Maximum Depth (cm)	Surface Area (m²)	Duration (# days)	% Canopy Cover
managed	42 ± 15 a	548 ± 375 a	65 ± 28 a	48 ± 34 ab
roadside	59 ± 37 a	214 ± 169 b	65 ± 31 a	28 ± 24 a
unmanaged	50 ± 26 a	529 ± 303 a	62 ± 40 a	77 ± 25 b

Table 4. Total numbers of breeding adults of 10 amphibian species detected during time-constrained surveys of 10 managed, 10 roadside, and 10 unmanaged ephemeral pools surveyed between 12 May and 14 June in 1996 and 1997, in Algonquin Provincial Park, Ontario.

Pool Type	AMLA	AMMA	PLCI	BUAM	HYVE	PSCR	RASY	RACL	RASE	RACA	Total
1996											
managed	0	0	5	22	4	63	29	13	1	2	139
roadside	0	0	2	6	1	117	34	19	0	1	180
unmanaged	1	2	8	15	0	136	105	47	1	0	315
Total	1	2	15	43	5	316	168	79	2	3	634
1997											
managed	1	0	3	198	0	95	65	66	0	0	428
roadside	1	1	0	90	0	106	17	15	0	0	230
unmanaged	1	1	3	36	0	151	33	10	0	0	235
Total	3	2	6	324	0	352	115	91	0	0	893

(AMLA=*Ambystoma laterale*; AMMA=*Ambystoma maculatum*; PLCI=*Plethodon cinereus*; BUAM=*Bufo americanus*; HYVE=*Hyla versicolor*; PSCR=*Pseudacris crucifer*; RASY=*Rana sylvatica*; RACL=*Rana clamitans*; RASE=*Rana septentrionalis*; RACA=*Rana catesbeiana*)

Table 5. Total numbers of Wood Frog (*Rana sylvatica*) and Spotted Salamander (*Ambystoma*) egg masses detected in 10 managed, 10 roadside, and 10 unmanaged ephemeral pools surveyed in Algonquin Provincial Park, Ontario, in 1996 and 1997.

Pool Type	Wood Frog		Spotted Salamander		Total	
	1996	1997	1996	1997	1996	1997
managed	88	5	55	0	143	5
roadside	294	1	48	14	342	15
unmanaged	87	1	61	0	148	1
Total	469	7	164	14	633	21

Table 6. Total numbers of larvae of 5 amphibian species detected during time-constrained surveys of 10 managed, 10 roadside, and 10 unmanaged ephemeral pools surveyed in 1996 and 1997, in Algonquin Provincial Park, Ontario.

Pool Type	*Ambystoma*	BUAM	PSCR	RASY	RACL	Total
1996						
managed	39	2893	217	1481	0	4630
roadside	7	38	16	11006	0	11067
unmanaged	20	0	26	3296	0	3342
Total	66	2931	259	15783	0	19039
1997						
managed	5	1854	17	75	0	1951
roadside	4	13024	25	2	33	13088
unmanaged	0	0	12	20	0	32
Total	9	14878	54	97	33	15071

(BUAM=*Bufo americanus*; PSCR=*Pseudacris crucifer*; RASY=*Rana sylvatica*; RACL=*Rana clamitans*)

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Table 7.   Decay classes of downed woody debris (after Chambers and Lee 1992).

Decay Class	Description
1	bark, branches, and texture of the log intact, log elevated off the ground by its branches
2	bark and texture of log mostly intact, branches gone, log elevated on support points, but slightly sagging
3	trace bark left on log, wood disintegrating into large chunks, colour of wood is faded, log sagging on the ground
4	bark and branches completely disintegrated, wood has disintegrated to soft, blocky pieces and has faded to a brown or yellowish colour, log is resting completely on the ground
5	wood has disintegrated further to a powdery texture and yellowish to grey colour, log is sinking into the ground

Table 8. Total numbers of 6 species of amphibians detected during area-constrained quadrat surveys of 10 managed and 10 unmanaged forest stands surveyed in 1996 and 1997, in Algonquin Provincial Park, Ontario.

Stand Type	AMLA	PLCI	BUAM	PSCR	RASY	RACL	Total
1996							
managed	0	50	10	1	0	1	62
unmanaged	0	73	15	3	3	0	94
Total	0	123	25	4	3	1	156
1997							
managed	1	63	28	2	1	0	95
unmanaged	0	59	5	4	0	0	68
Total	1	122	33	6	1	0	163

(AMLA=*Ambystoma laterale*; PLCI=*Plethodon cinereus*; BUAM=*Bufo americanus*; PSCR=*Pseudacris crucifer*; RASY=*Rana sylvatica*; RACL=*Rana clamitans*)

Table 9. Total numbers of 7 species of amphibians detected during surveys of drift fence and pitfall trap arrays in 10 managed and 10 unmanaged forest stands over 57 array nights (23 June - 28 August) during the summer of 1996, 46 array nights (17 September - 1 November) during the fall of 1996, and 42 array nights (18 May - 7 July) during the spring of 1997, in Algonquin Provincial Park, Ontario.

Stand Type	NOVI	AMLA	AMMA	PLCI	BUAM	RASY	RACL	Total
Summer 1996								
managed	1	0	2	2	996	11	0	1012
unmanaged	0	0	0	7	451	18	1	477
Total	1	0	2	9	1447	29	0	1489
Fall 1996								
managed	2	1	2	2	24	4	0	35
unmanaged	0	1	4	8	11	6	0	30
Total	2	2	6	10	35	10	0	65
Spring 1997								
managed	0	7	2	1	222	4	0	236
unmanaged	1	3	12	1	101	2	0	120
Total	1	10	14	2	323	6	0	356

(NOVI=*Notophthalmus viridescens*; AMLA=*Ambystoma laterale*; AMMA=*Ambystoma maculatum*; PLCI=*Plethodon cinereus*; BUAM=*Bufo americanus*; RASY=*Rana sylvatica*; RACL=*Rana clamitans*)
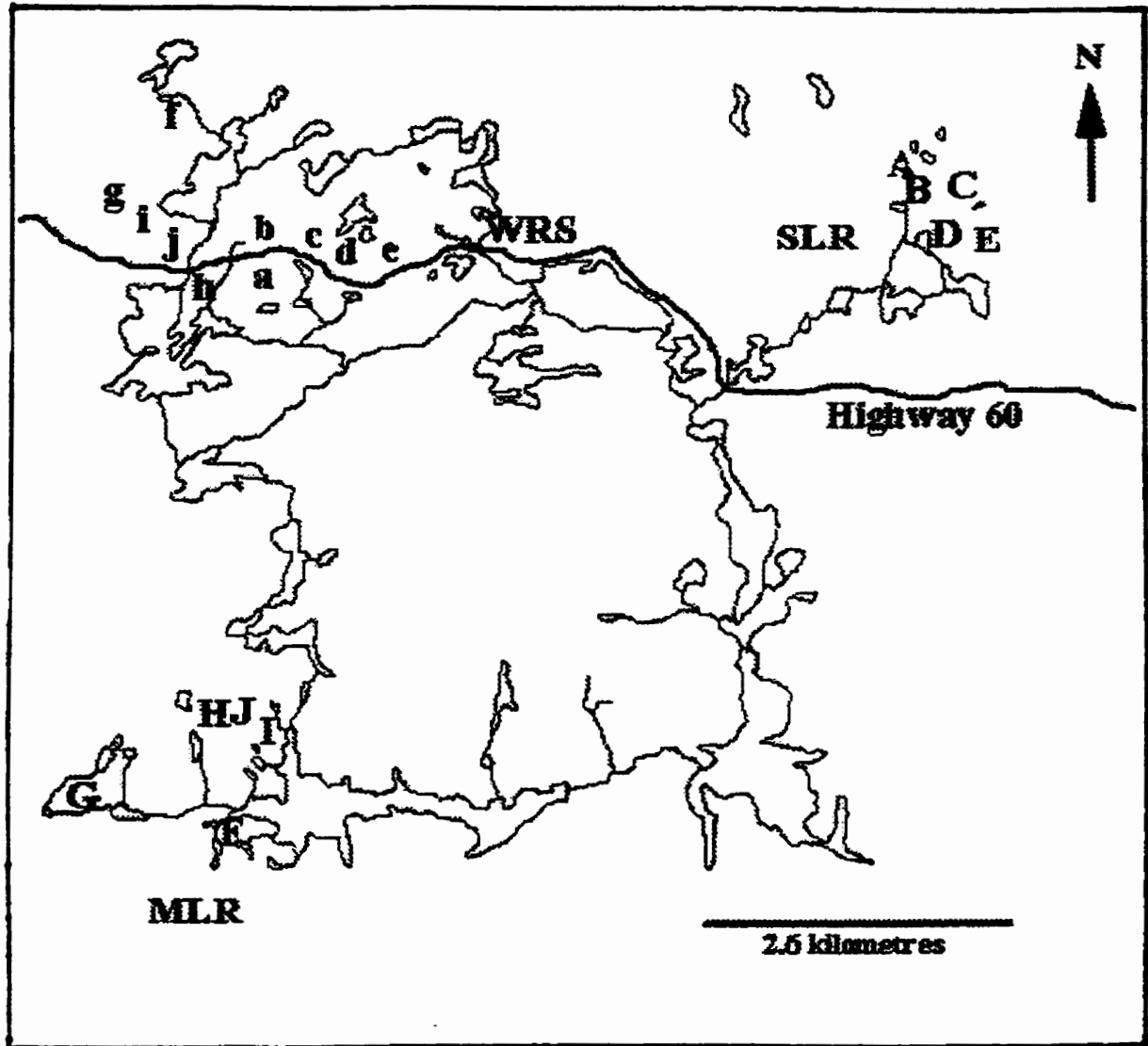
Figure 1. Location and sampling sequence of managed and unmanaged forest stands surveyed in Algonquin Provincial Park, Ontario. Managed stands A-E in the Sunday Lake Road (SLR) area of the Park were paired with unmanaged stands a-e along the Highway 60 corridor (H60), and were surveyed in 1996. Managed stands F-J in the Martin Lake Road (MLR) area of the Park were paired with unmanaged stands f-j along the Highway 60 corridor, and were surveyed in 1997. Managed and unmanaged forest stands indicated with the same letter (e.g. A and a) were sampled concurrently, as a pair.

MLR-3489
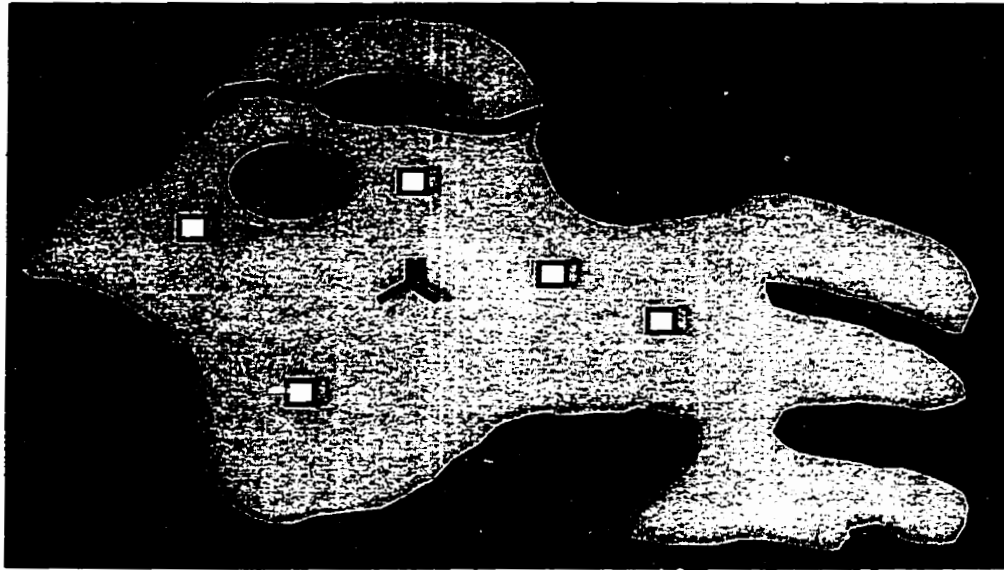
H60-6701
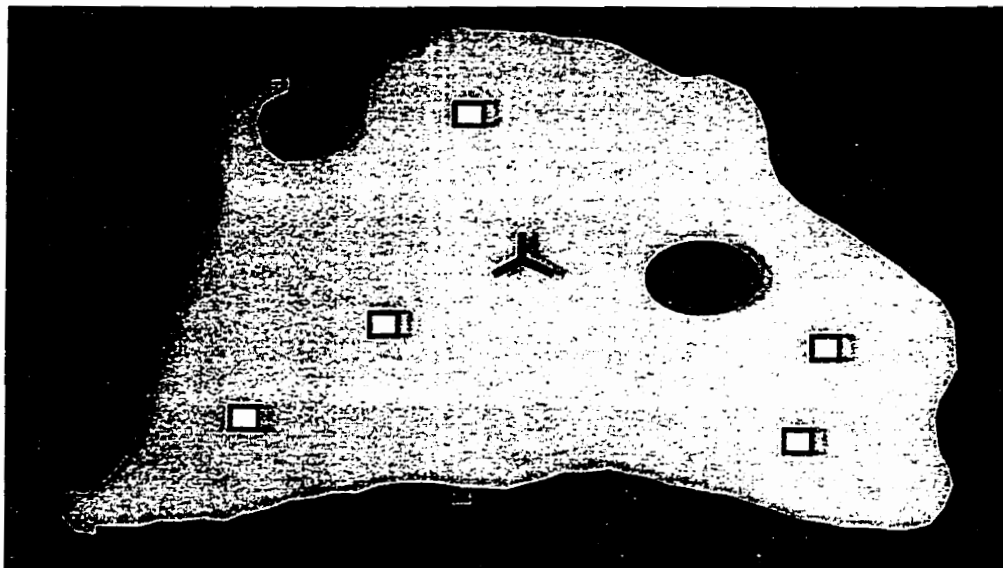
Figure 2. Schematic diagram of representative managed (MLR-3489) and unmanaged (H60-6701) shade-tolerant hardwood forest stands selected as study sites. Within each managed and unmanaged forest stand were located a drift fence and pitfall trap array (at each stand's center), and 5 (10 x 10 m) quadrats (randomly located throughout each stand). A managed and a roadside ephemeral pool were located within each managed forest stand, and an unmanaged ephemeral pool was located within each unmanaged forest stand.
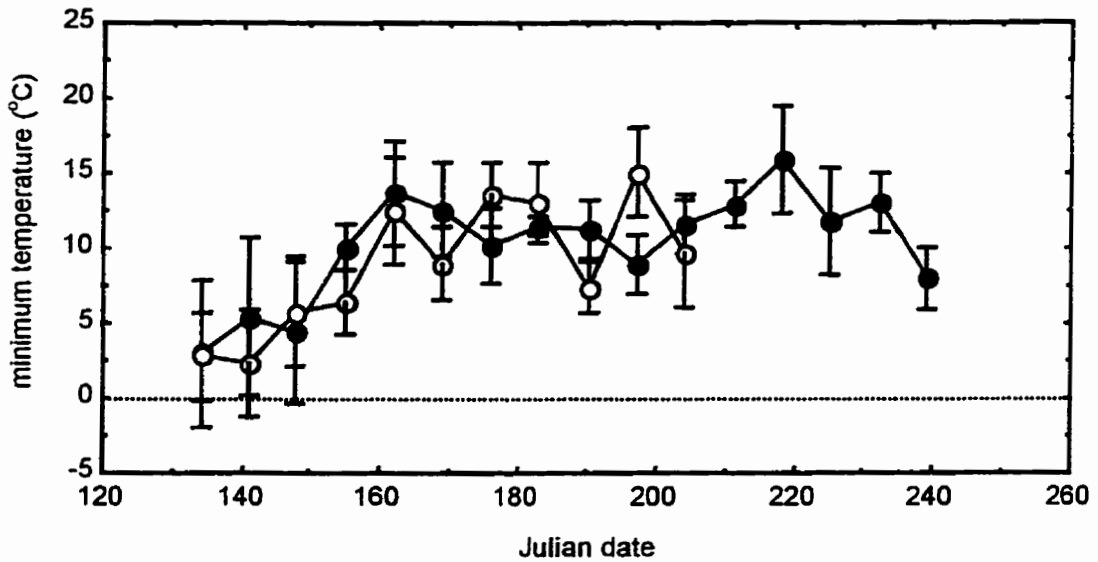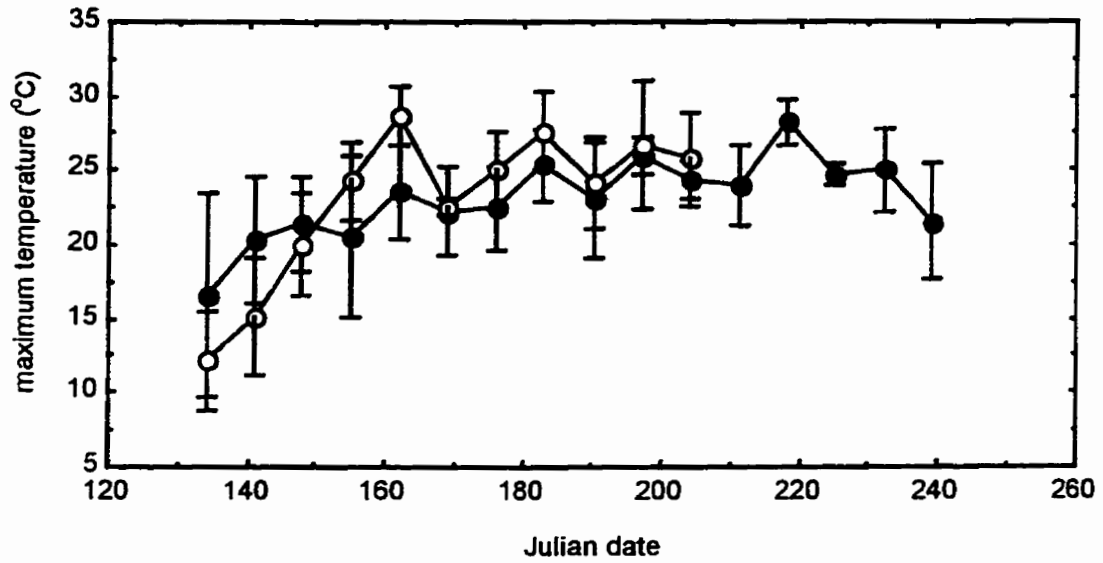
Figure 3. Average weekly maximum and minimum air temperatures (°C) taken at the Wildlife Research Station in Algonquin Provincial Park, Ontario. Indicated are seven-day averages (mean ± SD) of temperatures taken between the 12 May and 31 August of 1996 (●) and between the 11 May and 5 August of 1997 (○).
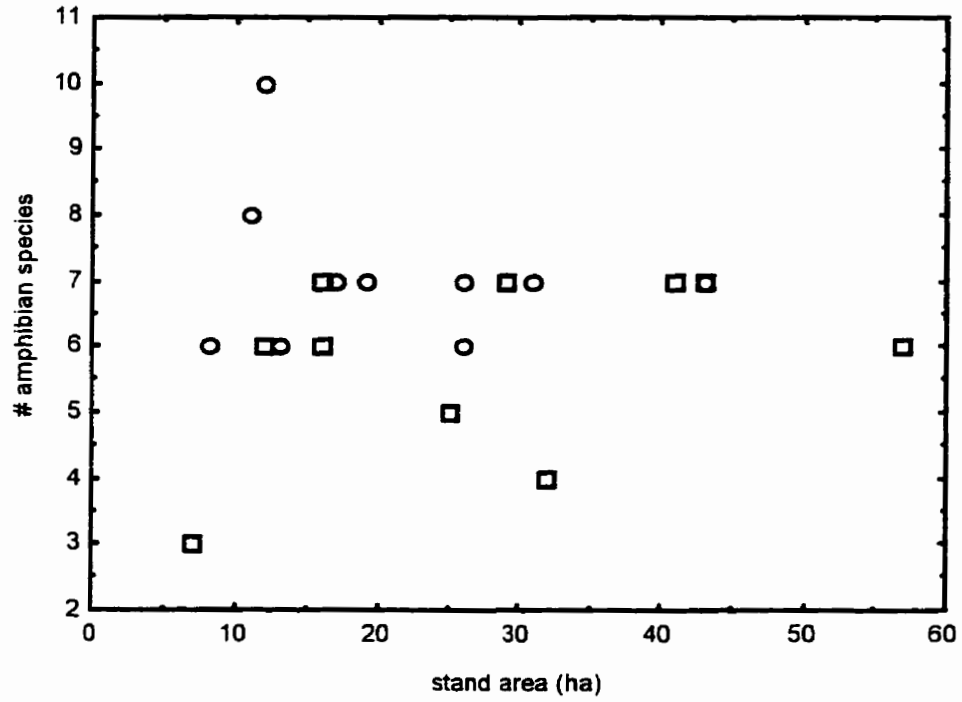
Figure 4. Number of amphibian species detected in 10 managed (○) and 10 unmanaged (□) forest stands of different sizes in Algonquin Provincial Park, Ontario.
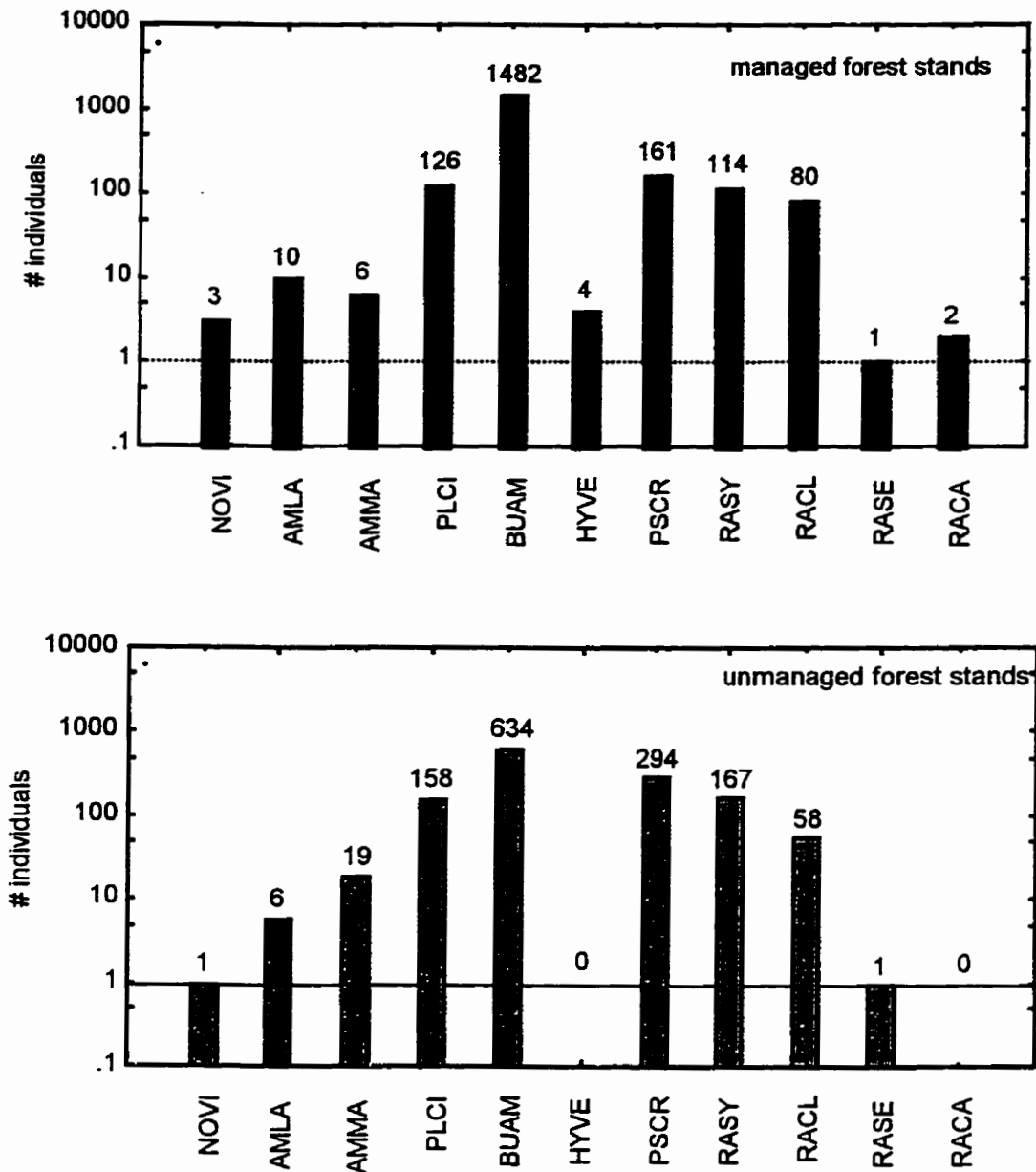
Figure 5. Heterogeneity of amphibian communities in 10 managed (dark hatching) and 10 unmanaged (light hatching) forest stands of Algonquin Provincial Park, Ontario. The total number of juvenile and adult individuals of each species detected during surveys of managed and unmanaged ephemeral pools, quadrats, and drift fence and pitfall trap arrays, is indicated and plotted on a logarithmic scale. NOVI=*Notophthalmus viridescens*; AMLA=*Ambystoma laterale*; AMMA=*Ambystoma maculatum*; PLCI=*Plethodon cinereus*; BUAM=*Bufo americanus*; HYVE=*Hyla versicolor*; PSCR=*Pseudacris crucifer*; RASY=*Rana sylvatica*; RACL=*Rana clamitans*; RASE=*Rana septentrionalis*; RACA=*Rana catesbeiana*.

Figure 6. Minimum temperature (°C) over time in 10 managed (●) (third-degree polynomial regression: $y=3762.449-73.211x+0.473x^2-0.001x^3$; $r^2=0.675$), 10 roadside (▼) (simple linear regression: $y=0.218x-24.154$; $r^2=0.582$), and 10 unmanaged (□) (third-degree polynomial regression: $y=6989.635-133.878x+0.852x^2-0.002x^3$; $r^2=0.511$) ephemeral pools in Algonquin Provincial Park, Ontario. Temperatures were taken between 18 May and 29 June for pools surveyed in both 1996 and 1997. Indicated for the simple linear regression of minimum temperature over time in roadside pools only, are the 95 percent confidence limits for the slope of the regression line, and the 95 percent confidence bands for the true mean of minimum temperature over time.

managed pools

roadside pools
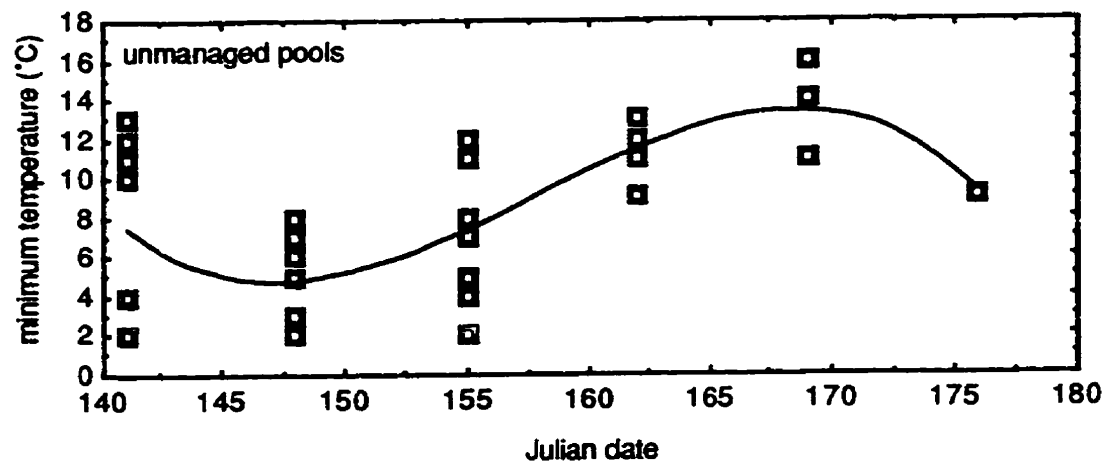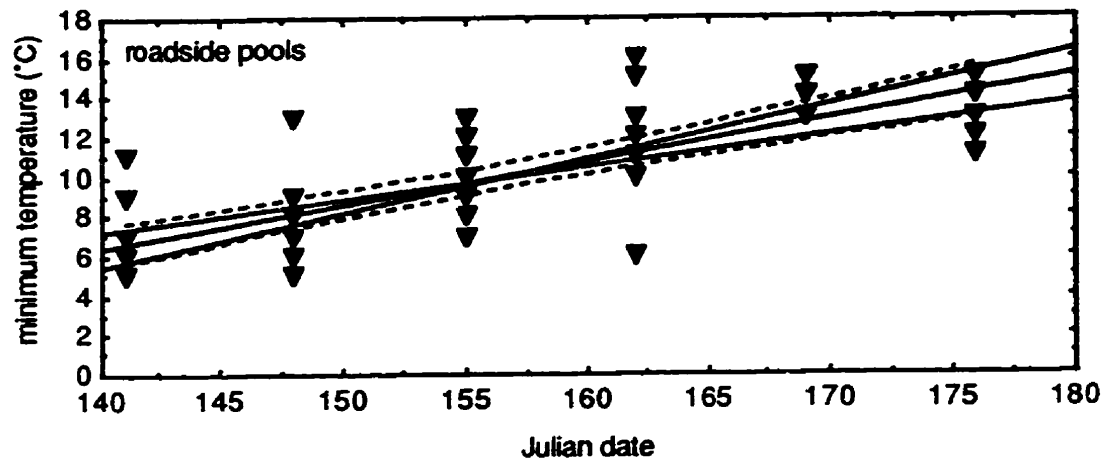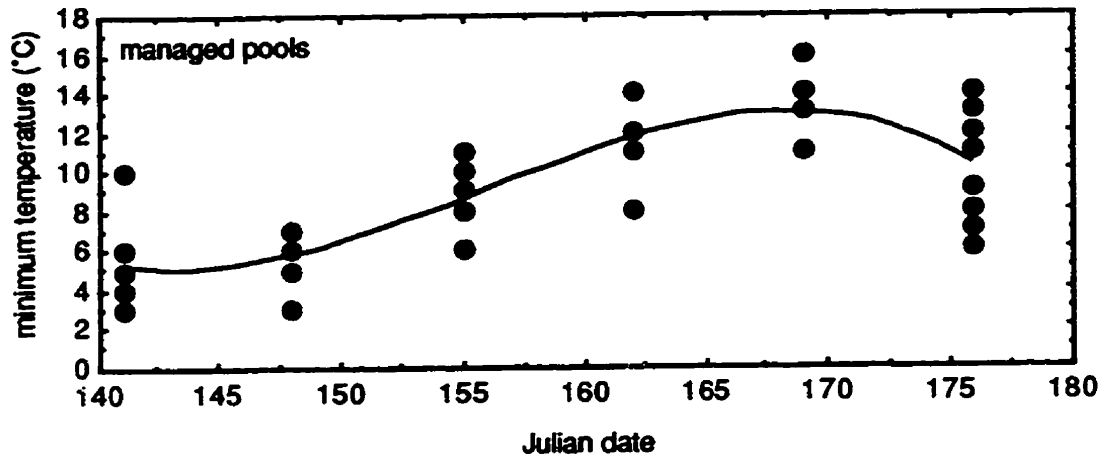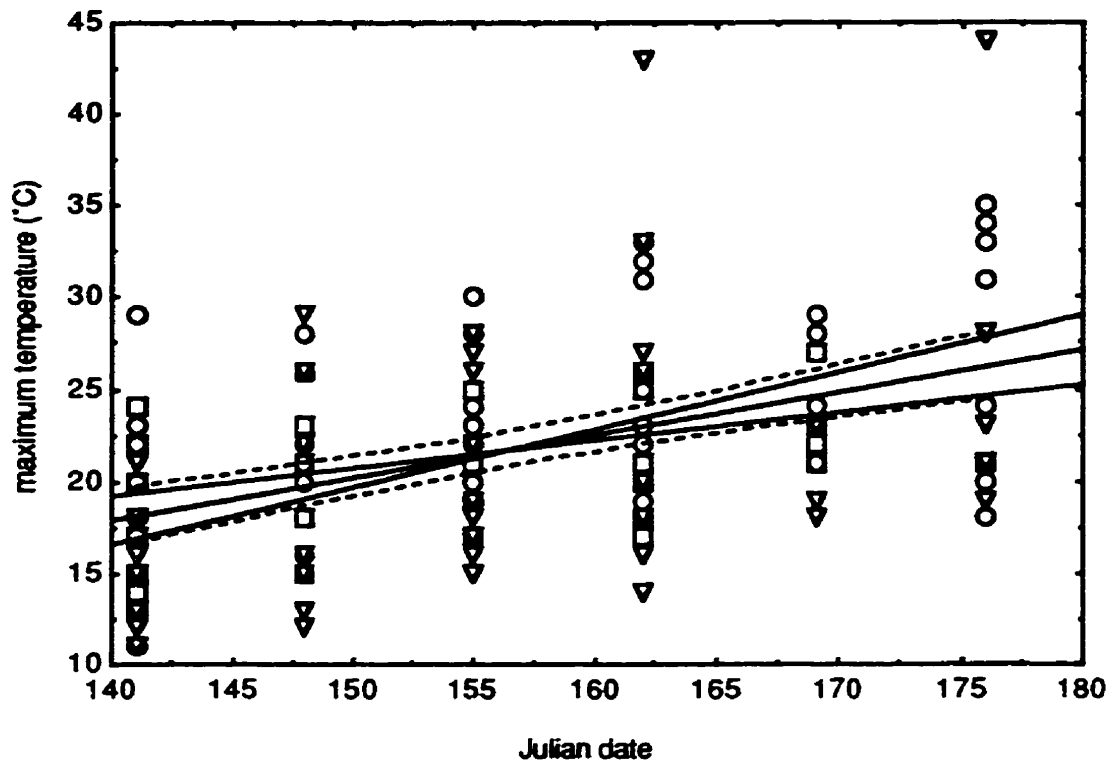
unmanaged pools

Figure 7. Simple linear regression of maximum temperature (°C) over time common to managed (O), roadside (u) and unmanaged (□) ephemeral pools in Algonquin Provincial Park, Ontario (y=0.23x-14.29; r²=0.201). Temperatures were taken between 18 May and 29 June for pools surveyed in both 1996 and 1997. Indicated are the 95 percent confidence limits for the slope of the regression line and the 95 percent confidence bands for the true mean of maximum temperature over time.
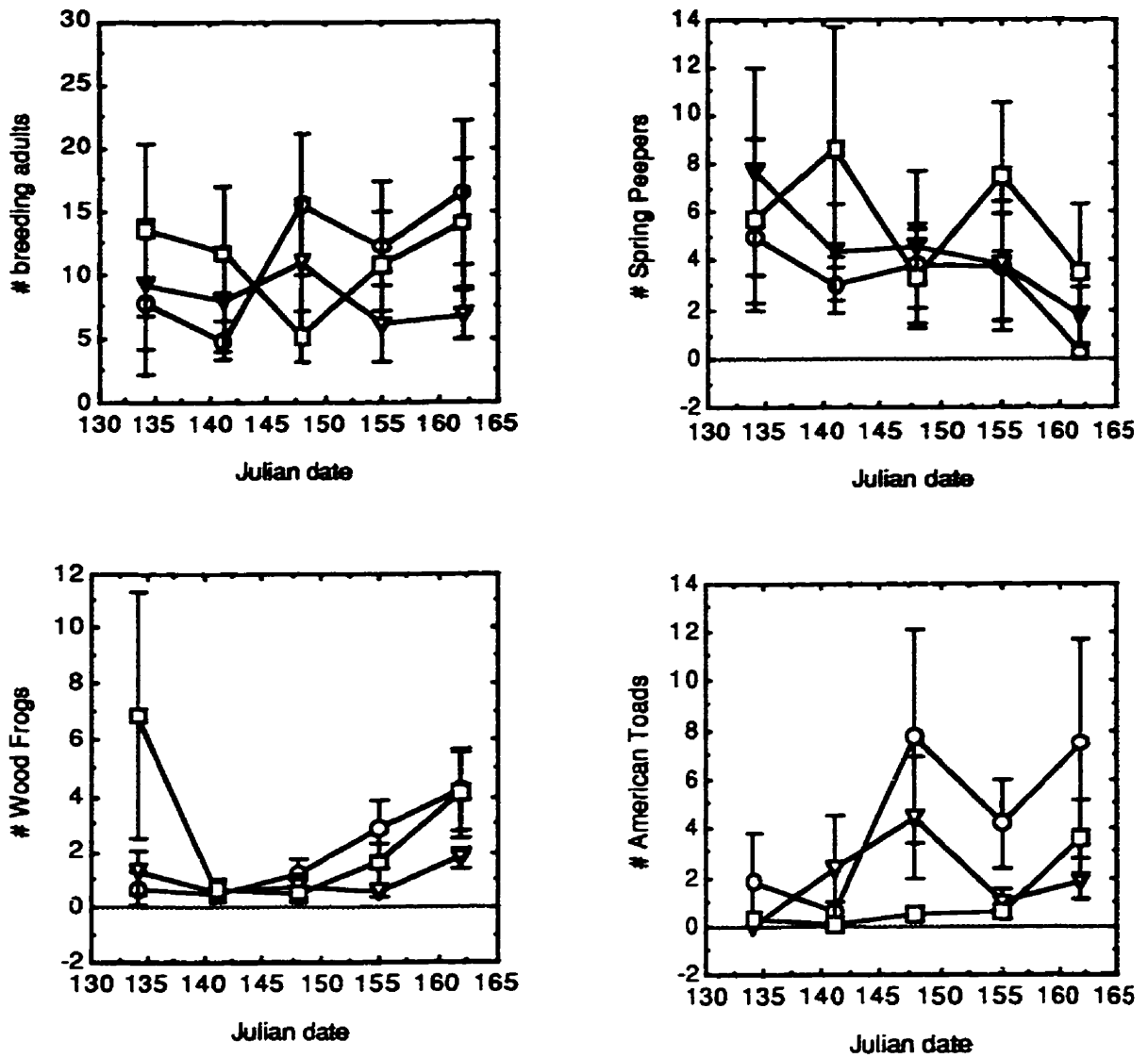
Figure 8. Abundance (mean number of individuals ± SE) of breeding adults, Spring Peepers (*Pseudacris crucifer*), Wood Frogs (*Rana sylvatica*), and American Toads (*Bufo americanus*), in 10 managed (O), 10 roadside (u) and 10 unmanaged (□) ephemeral pools over the breeding season (12 May - 14 June 1996 and 1997) in Algonquin Provincial Park, Ontario.

102
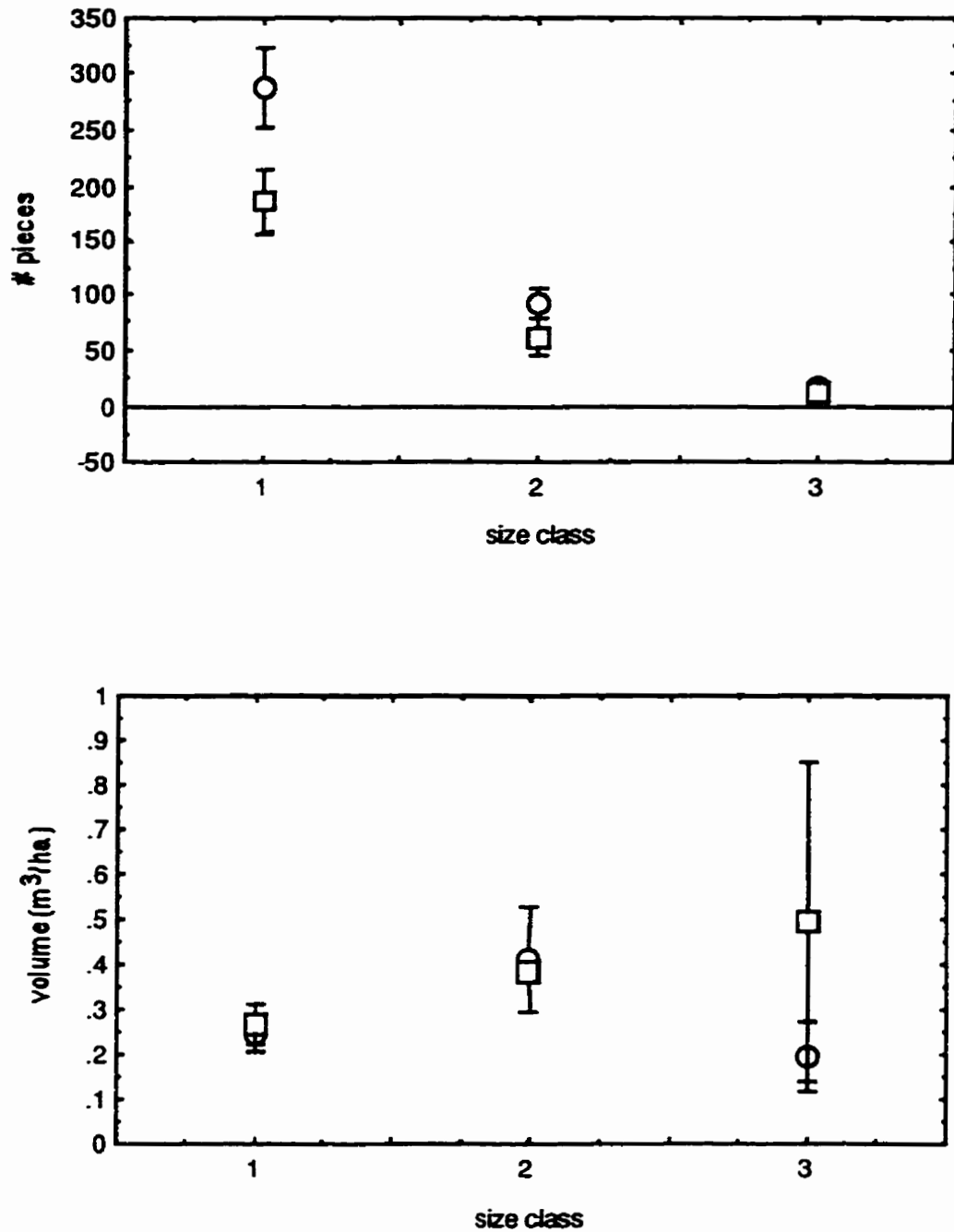
Figure 9. The mean (± SE) number of pieces and volume (m³) of downed woody debris per hectare of 10 managed (O), and 10 unmanaged (□) shade-tolerant hardwood forest stands, in size classes 1 (pole logs: 7.5 cm < diameter < 24 cm), 2 (saw logs: 24 cm < diameter < 50 cm), and 3 (mature logs: diameter > 50 cm), in Algonquin Provincial Park, Ontario.

Figure 10. The mean ($\pm$ SE) number of pieces (/ha) and volume (m^3/ha) of pole- (7.5 cm < diameter < 24 cm), saw- (24 cm < diameter < 50 cm), and mature-sized (diameter > 50 cm) downed woody debris in decay classes 1 through 5 in 10 managed (O) and 10 unmanaged (□) forest stands in Algonquin Provincial Park, Ontario

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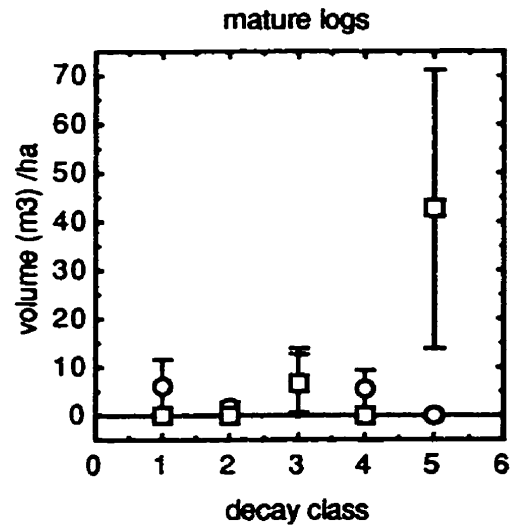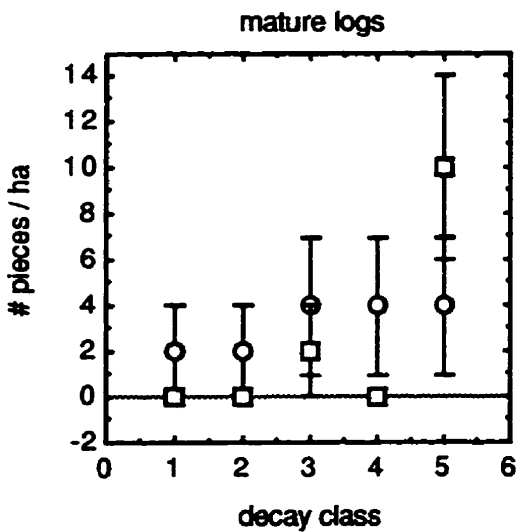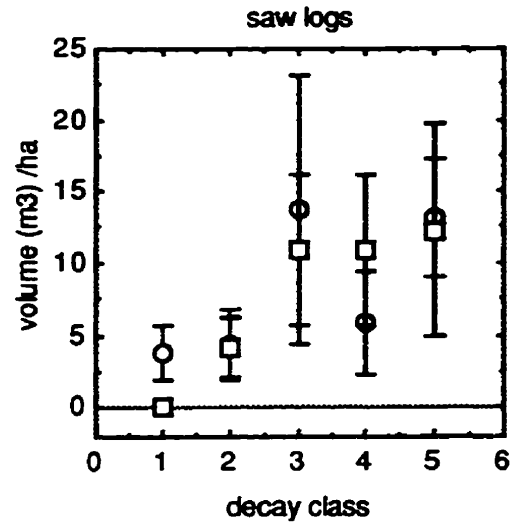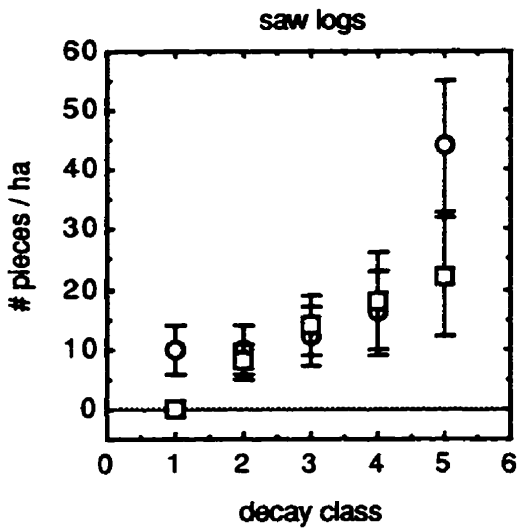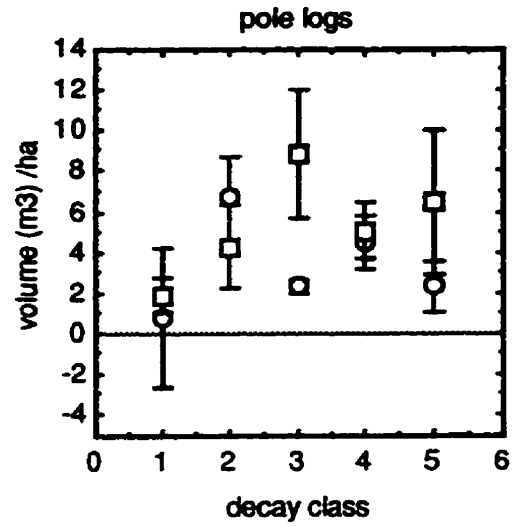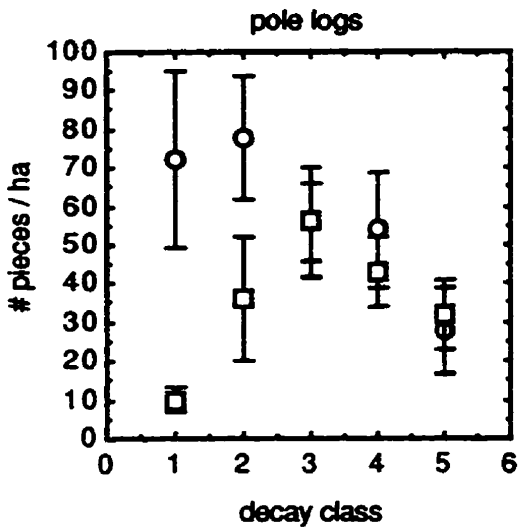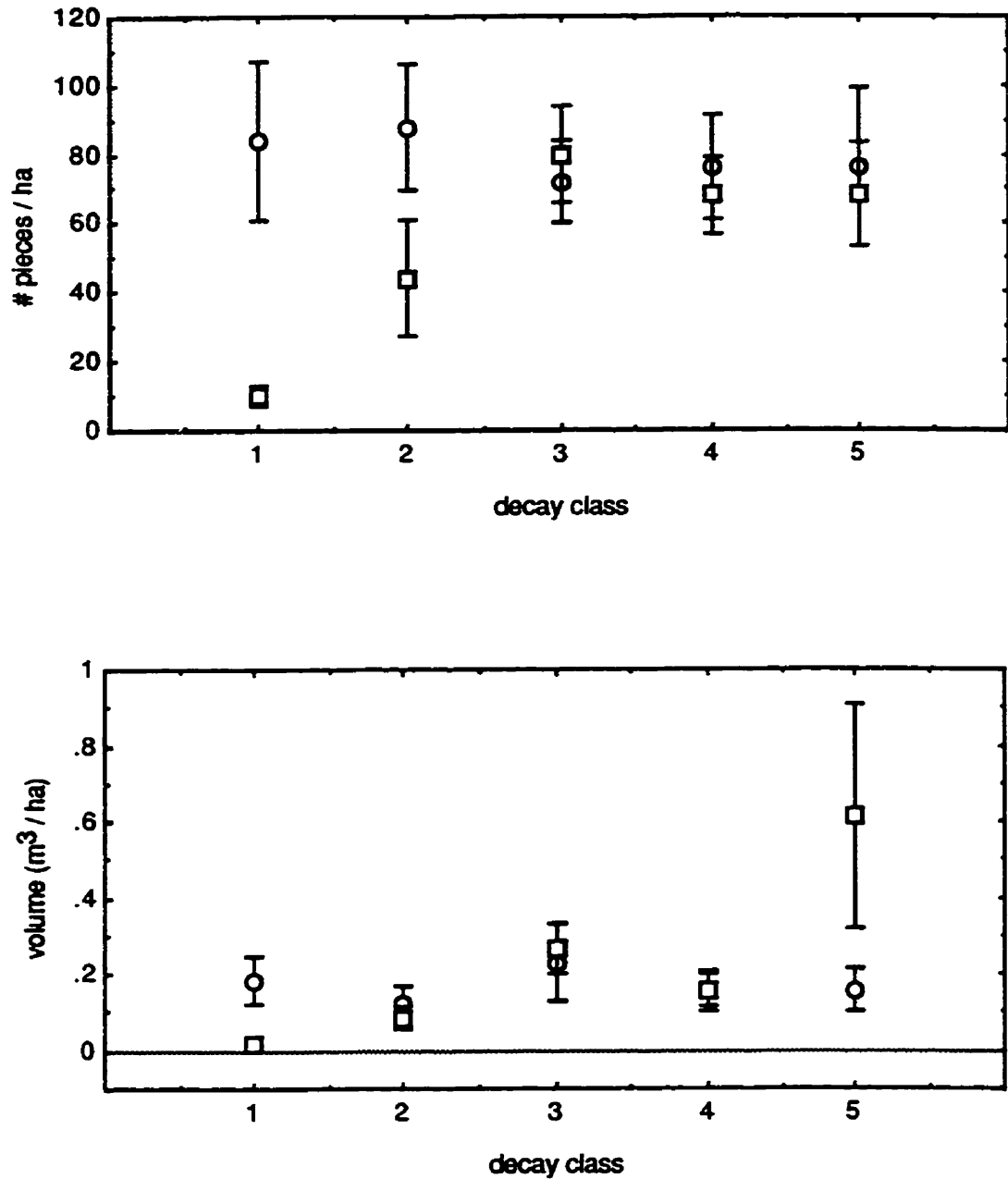
Figure 11. The mean ($\pm$ SE) number of pieces and volume (m^3) of downed woody debris per hectare of 10 managed (O) and 10 unmanaged (□) forest stands, in decay classes 1 through 5, in Algonquin Provincial Park, Ontario.
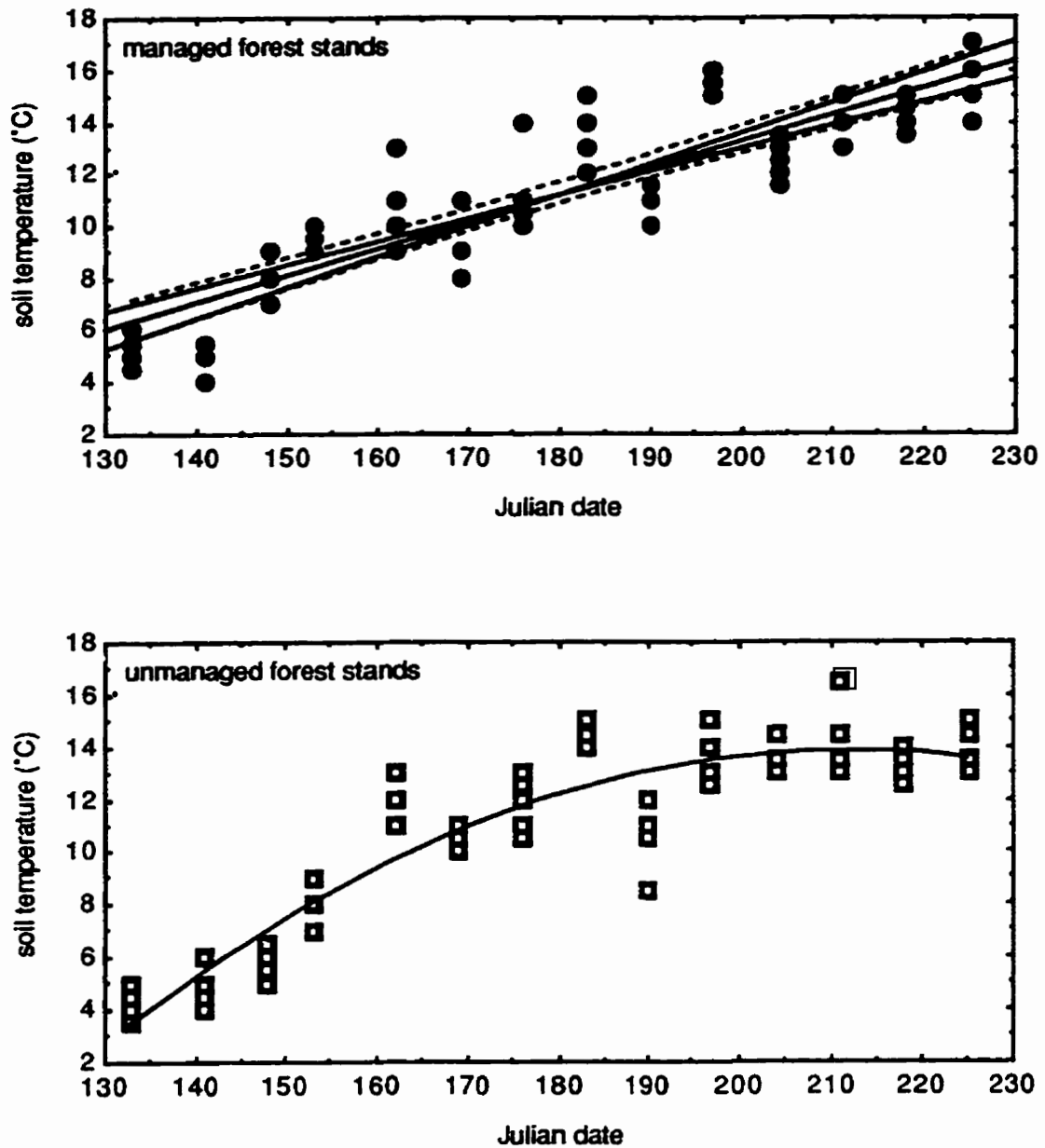
Figure 12. Relationships of soil temperature (°C) over time in 5 managed (●) (simple linear regression: y=0.104x-7.441; r^2=0.0741) and 5 unmanaged (□) (second-degree polynomial regression: y=0.719x-0.002x^2-62.101; r^2=0.858) forest stands surveyed between 11 May and 16 August 1997, in Algonquin Provincial Park, Ontario. Indicated for the simple linear regression of soil temperature over time in managed stands only, are the 95 percent confidence limits for the slope of the regression line, and the 95 percent confidence bands for the true mean of soil temperature over time.
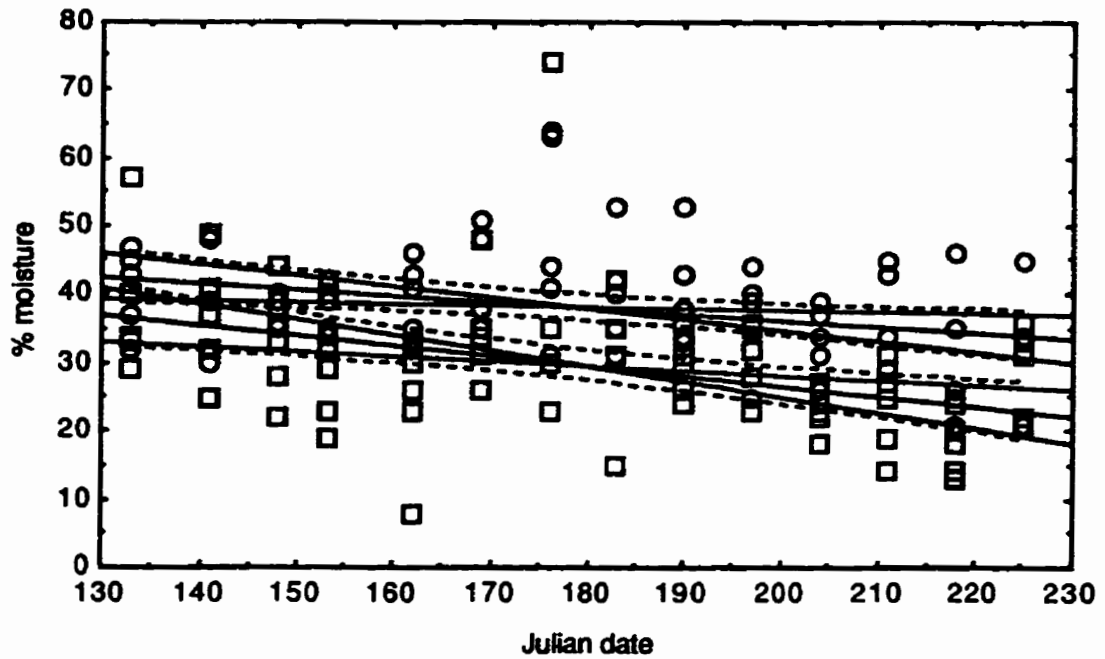
Figure 13. Simple linear regressions of soil moisture over time in 5 managed (O) (upper line: y=54.68-0.092x; r^2=0.097) and 5 unmanaged (□) (lower line: y=56.464-0.149x; r^2=0.172) forest stands surveyed between 11 May and 16 August 1997, in Algonquin Provincial Park, Ontario. Indicated for each regression line are the 95 percent confidence limits for the slope and the 95 percent confidence bands for the true mean of soil moisture over time.
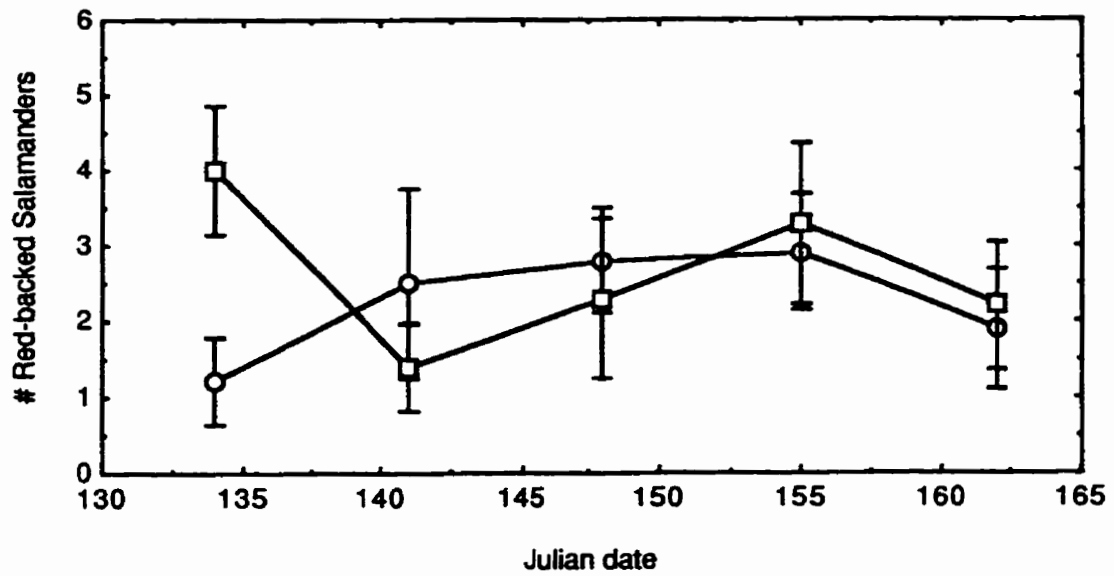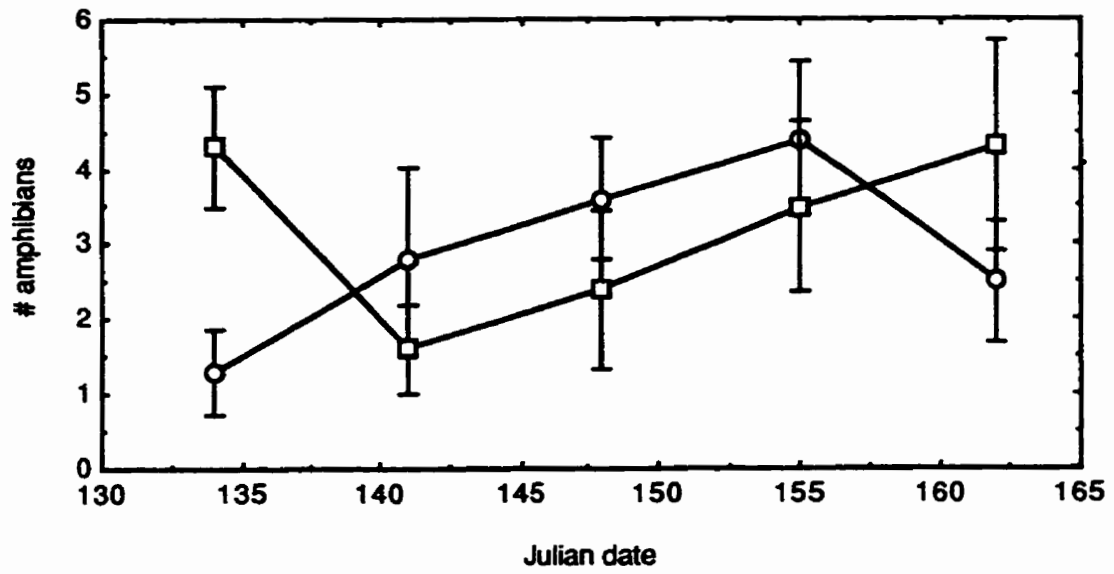
Figure 14. Abundance (mean number of individuals ± SE) of amphibians and Red-backed Salamanders (*Plethodon cinereus*) detected during area-constrained quadrat surveys of 10 managed (O) and 10 unmanaged (□) forest stands surveyed between 12 May and 14 June in both 1996 and 1997, in Algonquin Provincial Park, Ontario.

Figure 15. Abundance (mean number of individuals ± SE) of American Toads (*Bufo americanus*) detected during surveys of drift fence and pit fall trap arrays in 5 managed (O) and 5 unmanaged (□) forest stands throughout the summer (23 June - 28 August) and fall (17 September - 1 November) field seasons of 1996, and the spring (18 May - 7 July) field season of 1997, in Algonquin Provincial Park, Ontario.
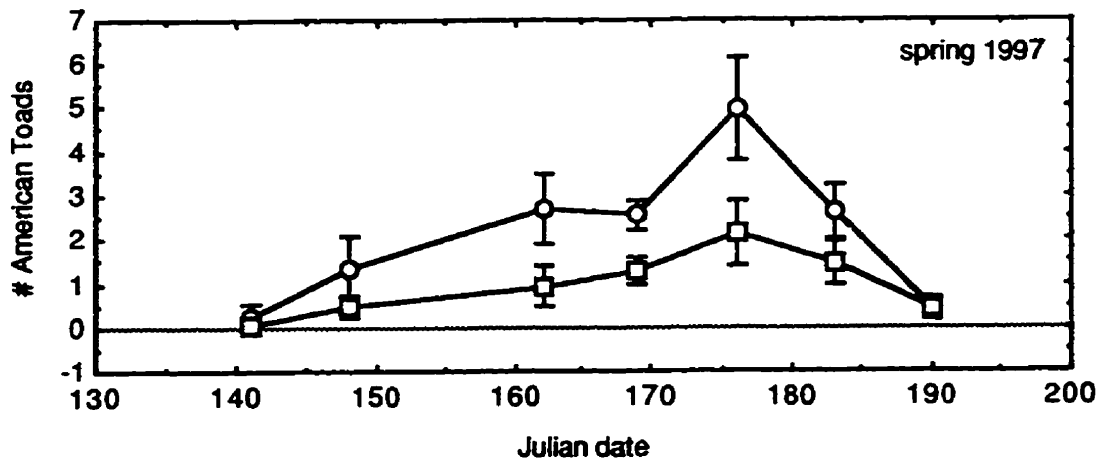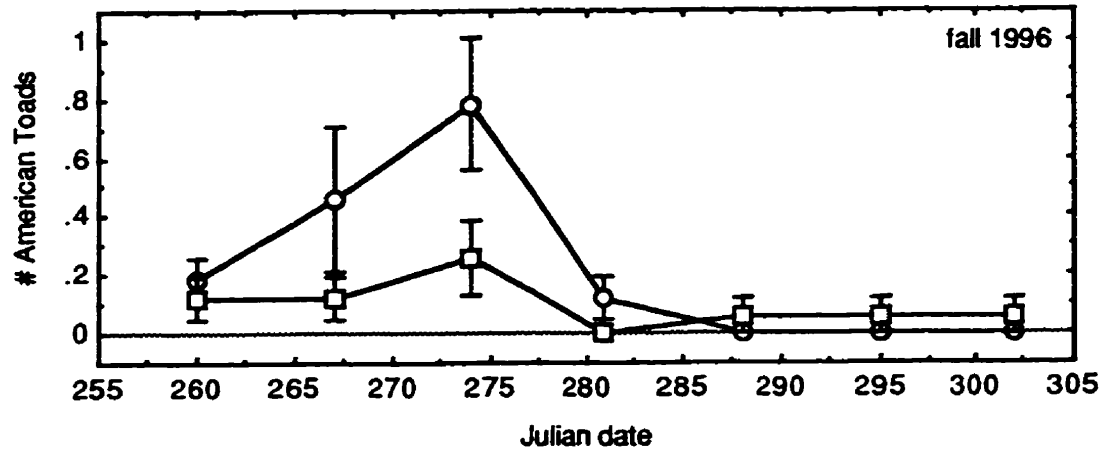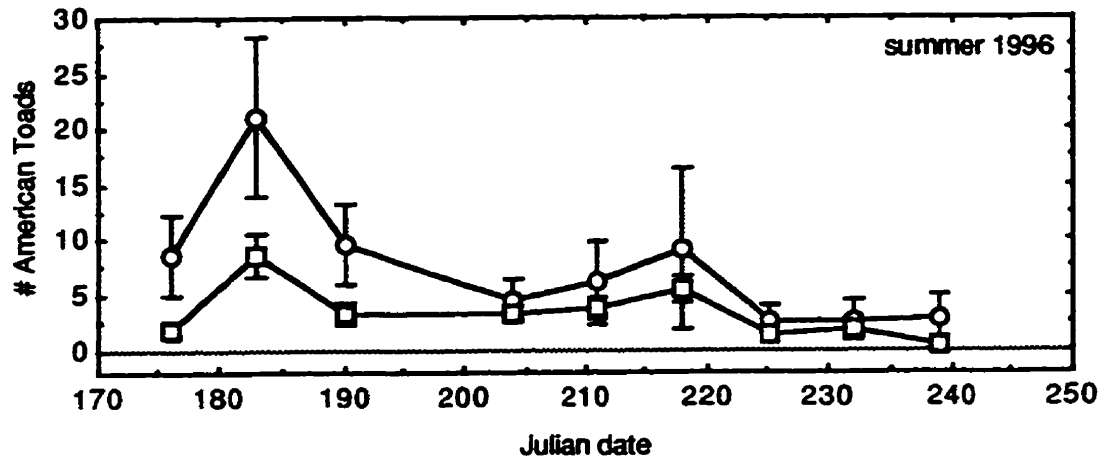
IMAGE EVALUATION
TEST TARGET (QA-3)

150mm

6"