HABITAT ASSOCIATIONS OF WOOD FROGS (*RANA SYLVATICA*), AND EFFECTS OF FRAGMENTATION, IN BOREAL MIXEDWOOD FORESTS

by

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ABSTRACT

I studied the habitat associations of wood frogs (*Rana sylvatica*) and fragmentation in boreal mixedwood forests of north-central Alberta. I sampled wood frogs, measured habitat characteristics, and assessed the general wetness of 10 sites from 1993 to 1995. The 10 sampling sites were in continuous forest in 1993, but through forest harvesting, six of these sites were made isolated fragments surrounded by 200-m wide clear cuts in 1994. The abundance of wood frogs decreased and average body length increased within 10-ha fragments two years post-harvesting compared to 100-ha and control sites. Forest fragmentation reduces the number of wood frogs, especially impacting small individuals, but the presence of wet patches within a site may mitigate the effects. Analyses of habitat indicate that wood frogs are associated with some characteristics of boreal mixedwood forests, perhaps most closely related to coarse woody material (CWM) approximately 5<11 cm in diameter. CWM of this size class is correlated with trembling aspen (*Populus tremuloides*) that is 23<38 cm diameter at breast height (dbh). I recommend further research into the effects of timber harvesting on migration and dispersal of amphibians, and for determining habitat requirements of amphibians at stand and landscape levels in boreal mixedwood forests.

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CHAPTER I

GENERAL INTRODUCTION

Historically, ecological research about the management and preservation of amphibian populations has lagged well behind that of other taxonomic groups, especially mammals and birds (Gibbons, 1988). However, amphibian research has increased significantly in the past decade, in part from concerns over their declining populations worldwide, and in part because of recent mandates for preserving biodiversity. To be useful to resource management, much of the current ecological research on amphibians has focused on the proximate causes of species' declines, the effects of habitat disturbance, and amphibian habitat requirements.

Amphibian populations fluctuate extensively from year to year (Berven, 1995), and this has sparked debate about whether declining amphibian populations witnessed today are as widespread or as serious as they appear (Pechman *et. al.*, 1991; Blaustein *et. al.*, 1994c). Because there are very few long term studies which capture the inherent variability of amphibian populations, our ability to determine the extent of this problem is hampered (Blaustein *et. al.*, 1994c). Declines in amphibian populations have occurred worldwide in pristine, as well as disturbed, environments (Barinaga, 1990; Blaustein and Wake, 1990; Phillips, 1990). Evidence suggests that even species which were once considered numerous can decrease dramatically to critical population levels, or to extinction, within a relatively short period. Examples in western North America include the northern leopard frog (*Rana pipiens*) and spotted frog (*Rana pretiosa*), which have decreased rapidly in some areas within the last 20 years (Corn and Fogleman, 1984; Orchard, 1992). These trends concern scientists, because amphibians contribute significantly to the biomass of many ecosystems (Pough *et. al.*, 1987) and may serve as good indicators of environmental health (Phillips, 1990). Due to the uncertainty surrounding the stability of many amphibian populations at this time, guidelines established for their management should be conservative and cautious.

Hypotheses advanced to explain amphibian population declines include increased ultraviolet radiation exposure at the larval stage (Blaustein *et. al.*, 1994a), spread of a pathogenic fungal disease (Blaustein *et. al.*, 1994b), overharvesting, predation from introduced species, and increased toxins in the environment (Blaustein and Wake, 1990; Phillips, 1990). One of the major causes of amphibian declines is believed to be the degradation and loss of habitat (Johnson, 1992). In North America, habitat loss for amphibians has largely resulted from the clearing and draining of land for agriculture, urban development, and from forest harvesting.

In some areas, second-growth habitats which result from forest harvesting have lower species richness and abundance of amphibians than do late successional forests (e.g., Pough *et al*, 1987; Welsh, 1990; Petranka *et. al.*, 1994; Dupuis *et. al.*, 1995). The permeable skin of amphibians impose unique physiological constraints on their ability to exploit various habitats (Adolph, 1932). They are restricted to moist habitats which permit gas exchange and reproduction without dehydration (Zug, 1993). The forest environment, especially old-growth forests, provide protective cover and stable climatic conditions for amphibians (Heatwole, 1962; Welsh, 1990), but increasing land-use pressures on old-growth forests, as well as increasing proportions of second-growth habitat, may seriously threaten amphibian populations. The landscapes being created today have never existed before. The ability of organisms to adapt to increasing proportions of second-growth habitat, and fragmentation of old-growth forests, will influence community composition everywhere (Kellman, 1996).

An example of an ecosystem facing vast changes in the coming decades is the boreal forest. This is one of the last large, relatively pristine ecosystems left in North America.

Nonetheless, there is increasing pressure to harvest boreal mixedwood forests for the pulp and paper industry. As this ecosystem is exploited, the landscape will become fragmented, and the landscape composition and configuration will be dramatically altered (e.g., increased proportions of early and mid-successional stands compared to old-growth forests, and cutblocks more rectangularly shaped, and of different sizes, compared to areas cleared naturally by fire). Concern over this dramatic large-scale harvest has prompted the initiation of a series of studies investigating the effects of timber harvesting on biodiversity in boreal mixedwood forests (Schmeigelow and Hannon, 1993; Stelfox, 1995). At Calling Lake, Alberta, a large collaborative study has been initiated to investigate the effects of fragmentation on biodiversity (Schmeigelow and Hannon, 1993). The majority of the work at Calling Lake focuses on birds, investigating species-area relations, breeding success, use of corridors, and habitat use. The research area contains four fragment sizes replicated three times each (i.e., 1, 10, 40 and 100-ha; surrounded by minimum 200-m wide clearcuts), as well as a large control area. Pre-treatment data were collected in 1993 when the research area was unharvested, and fragmentation occurred in winter 1993/94. In addition to the work being conducted on birds, effects of fragmentation on small mammal and amphibian populations have also been investigated. My research focused on wood frogs (*Rana sylvatica*), determining habitat associations of this species within boreal mixedwood forests, and effects of fragmentation.

Amphibians are an ideal taxonomic group for investigating the effects of landscape level disturbances, such as forest fragmentation. Compared to many other vertebrates, amphibians have relatively small home ranges and low vagility, which means that they will have to adapt or perish in the face of large-scale habitat disturbance. Many amphibian species depend upon both terrestrial and aquatic environments, migrating between them on an annual basis, while others may spend their entire life within one small area, such as a log (Zug, 1993). Both strategies are affected by forestry and habitat fragmentation. Those species which need to migrate between two or three habitat types depend upon unimpeded movement between these sites for their survival. Those species which move very little may not have the ability to successfully disperse to a new location following habitat disturbance, when, for example, microclimate conditions surrounding and within their log become unsuitable. The spatial distribution of suitable breeding sites, and of summer and winter ranges, will influence the distribution of amphibians within that environment. Forest practices change the configuration of suitable habitat types for amphibians (Welsh, 1990; Dupuis *et. al.*, 1995). Whether amphibians are flexible in their use of habitats and movement corridors is unknown, but high flexibility is unlikely when many species are found to return to natal breeding sites and summer ranges (e.g., Bellis, 1965; Berven, 1995). As a result, landscape level planning of the juxtaposition of harvested and unharvested areas, especially in relation to wet patches, will likely be a key factor in management strategies which seek to maintain source populations of amphibians.

Very little is known of the ecology of the amphibians which inhabit the boreal forest. Knowing what the potential impacts of forest harvesting may be for these species, and what their specific habitat requirements are, are essential for including amphibians in forest management guidelines. The objectives of this thesis were: 1) to determine the habitat associations wood frogs in the boreal mixedwood forest of Calling Lake, Alberta; and 2) to investigate effects of forest fragmentation on wood frogs within this ecosystem. From these findings, I make recommendations for further research that is needed to manage amphibian populations in boreal mixedwood forests.

CHAPTER II

HABITAT ASSOCIATIONS OF WOOD FROGS (*RANA SYLVATICA*) IN BOREAL MIXEDWOOD FORESTS

INTRODUCTION

The boreal forest is a complex ecosystem comprised of a fine-scale mosaic of habitats (Peterson and Peterson, 1992). This complex mosaic of different seral stages and species composition is believed to have resulted from fire and insect disturbances, which occurred in irregular patterns and shapes across the landscape (Bonan and Shugart, 1989). Strong and Leggat (1981) described the boreal forest as having a variety of forest ecoregions, reflecting plant species' responses to changes in topography, soils, and climatic variables across the landscape. One of these ecoregions is referred to as the 'boreal mixedwood'. Alberta contains more than 50% of Canada's boreal mixedwood forest, which covers about 40% of the province and approximately 290 000 km^2 (Rowe, 1972). In 1987 - 88, the government of Alberta leased 220 000 km^2 to the pulp and paper industry without conducting an environmental impact assessment (Nikiforuk and Struzik, 1989). Species which inhabit this ecosystem have presumably evolved to cope with the specific conditions and disturbance patterns found there (Bunnell, 1995). Little is known of the habitat associations and requirements of the five species of amphibians which inhabit this ecosystem (western toad - *Bufo boreas*; canadian toad - *Bufo hemiophrys*; northern leopard frog - *Rana pipiens*; wood frog - *Rana sylvatica*; and chorus frog - *Pseudacris triseriata*; Russell and Bauer, 1993). Amphibian habitat associations have been studied in a wide range of environments throughout most of North America, but few studies have taken place in the boreal forest of Canada.

In other parts of North America, numerous factors have been identified as influencing the presence, distribution, and abundance of amphibians. The main factors identified which influence the occurrence of terrestrial amphibians include the presence of standing water and/or moist air for breeding, rehydration, gas exchange, and escape from predators (Adolph, 1932; Pough *et. al.*, 1987). In addition to standing water, the density, structure and type of terrestrial vegetation contribute to moisture levels on the ground and in the air (Geiger, 1965; Heatwole, 1962). Apart from the need for moisture, other habitat requirements identified for many amphibian species include abundant prey, hibernation sites, and the presence of appropriate structural attributes (e.g., coarse woody material) to provide camouflage and protection from extreme climatic conditions (Jaeger, 1980; Aubry *et. al.*, 1988). Little is known of the habitat requirements of many amphibian species during the summer months away from breeding ponds, and especially during hibernation. The habitat attributes that amphibians require during these periods may be quite different from those they select for breeding, and may be just as critical to their survival. If breeding habitat alone is protected, only a portion of amphibian habitat requirements will be met. Management of forested ecosystems that support stable amphibian populations requires an understanding of all habitat needs.

Three species of amphibian are found in the Calling Lake research area: the wood frog, the western toad, and the chorus frog. The wood frog was selected as an ideal study species for investigating amphibian habitat associations in the boreal mixedwood forest because of its dependence on both terrestrial and aquatic environments, relative abundance in the area, and ready trappability compared to the other two species. The objective of this study was to identify habitat attributes of wood frogs in the boreal mixedwood forests of north-central Alberta, specifically 1) terrestrial attributes (i.e., vegetation, coarse woody material, canopy closure, and leaf litter depth), and 2) wetness attributes (i.e., percent wetness, number of wet patches, and variety of wet patches). Extensive timber extraction is occurring throughout the area and it is important that we identify key habitat attributes for various species, to plan appropriate juxtaposition of clearcuts, wet patches, and remaining forested habitat. This study provides information and recommendations for further research that will facilitate management decisions for maintaining stable amphibian populations in boreal mixedwood forests.

RESEARCH AREA AND SAMPLING SITES

The Calling Lake research area was established to study the effects of habitat fragmentation and timber extraction on biodiversity. The research area is located 250 km north of Edmonton and encompasses approximately 120 km^2 (12,000 ha) of boreal mixedwood forest. Early successional species in this ecoregion are trembling aspen (*Populus tremuloides*) and less importantly, balsam poplar (*Populus balsamifera*) and white birch (*Betula papyrifera*). Late successional species are mainly white spruce (*Picea glauca*) and to a lesser extent balsam fir (*Abies balsamea*). Jack pine (*Pinus banksiana*) communities occur on sandy sites; black spruce (*Picea mariana*) dominate poorly drained areas. Wetlands comprise about one quarter of the region (Strong and Leggat, 1981). Historically, insect outbreaks and fire have played an important role in creating the mosaic of stand types found in the boreal forest (Bonan and Schugart, 1989). All of the study sites at Calling Lake are in old stands (80 to 130 years since last disturbance) of aspen / mixedwood forest. The terrain in the research area has only minor variations in topography. The area has long, cold winters and relatively short, mild summers, with precipitation heaviest in July (Alberta Environmental Protection, 1996).

Selection of the Calling Lake area for the fragmentation project was based on a number of criteria, including its representativeness of the boreal mixedwood ecoregion, the planned harvesting schedule (i.e., to occur in winter 1993-94), and its similarity to those areas where biodiversity research was being conducted by the Alberta Environmental Centre (Schmiegelow and Hannon, 1993; Stelfox, 1995). The research area was unharvested, and baseline data were collected in 1993. It was subsequently winter logged in 1993 / 1994, with replicates of various sized fragments created that were surrounded by minimum 200-m wide clearcuts. A large control area, > 3500-ha, was left unharvested. Fragment sizes of 1, 10, 40 and 100-ha were replicated three times.

Time constraints and limited resources did not allow for sampling of amphibians in all study sites in 1993, thus only the 10-ha and 100-ha fragments (three replicates of each) and four control sites were sampled (n = 10). Preharvesting data were collected in July and August of 1993. In 1994 and 1995, six of the amphibian sampling sites were in isolated fragments, and sampling occurred from May to early August in both years. Four of the amphibian sampling sites were considered relatively 'younger' forest (80 - 90 years), and six were 'older' forest (110 - 130 years) according to Alberta Vegetation Inventory (AVI) mapping. All of the sites were primarily in aspen-dominated forest, however, some sites contained patches where the forest was dominated by white spruce (i.e., Sites C-1, T-2 , C-3; see Table 2.1 for site descriptions).

Table 2.1. Site descriptions for 10 amphibian sampling sites at Calling Lake, Alberta.

Sample Site	Approximate Age (years)	Fragment Site or Control	Wetness %	Wetness #*	Features Not Controlled For	General Habitat Features as Measured From 4 Vegetation Plots
T - 1	80 - 90	10-ha	0.00	0.0	- gas exploration cutline (GEC) along edge of grid	- high numbers of stems of alder (*Alnus crispa*) / willow (*Salix* sp.) shrubs, trembling aspen (1),** balsam poplar (1, 2); dense canopy
T - 2	110 - 130	10-ha	9.95	5.0	- GEC through grid - connected to 40-ha fragment along west side	- high numbers of stems of bracted honeysuckle (*Lonicera involucrata*), balsam poplar trees, CWM2***, litter depth, alder, total saplings (all species); relatively open canopy
T - 3	110 - 130	10-ha	0.00	0.0	- GEC through grid - no wet patches found within 200-m of fragment edge	- high numbers of stems of rose shrubs (*Rosa* sp.), black currant (*Ribes lacustre*), willow, balsam poplar, birch, white spruce saplings, trembling aspen (1), CWM1 - 4 combined
H - 1	80 - 90	100-ha	0.00	0.0	- GEC along edge of grid	- high numbers of stems of cranberry (*Viburnum edule*), trembling aspen (2, 3), white spruce (2), CWM3; dense canopy; low numbers of saplings of all species
H - 2	110 - 130	100-ha	0.24	2.7	- numerous GECs present	- high numbers of stems of balsam poplar (4), cranberry, CWM4, birch (1), raspberry (*Rubus ideaus*) , willow shrubs
H - 3	110 - 130	100-ha	0.00	0.0	- north facing slope through west part of grid	- high numbers of stems of bracted honey suckle, raspberry, black currant, balsam poplar, CWM4, litter depth, trembling aspen and balsam poplar saplings; relatively open canopy; low CWM1
C - 1	80 - 90	control	0.30	1.7	- southern end of area contains white spruce	- high numbers of stems of white spruce, rose shrubs, CWM3, trembling aspen (3); dense canopy
C - 2	80 - 90	control	0.46	2.3	- valley on east end of grid; leads down to old stream basin - GEC present	- high numbers of stems of alder shrubs and saplings, willow shrubs, CWM1 and 2, birch saplings, cranberry, snowberry (*Symphoricarpos occidentalis*), trembling aspen (1, 2); dense canopy
C - 3	110 - 130	control	4.14	4.7	- white spruce area along north and east side of grid - stream corridor along east end	- high numbers of stems of bracted honeysuckle, trembling aspen (3), white spruce (2, 4)
C - 4	110 - 130	control	0.46	5.7	- GEC along edge of grid	- high numbers of stems of red currant (*Ribes triste*), trembling aspen (4), birch (2), CWM4, willow, litter depth, trembling aspen and spruce saplings; relatively open canopy

* See Methods for a description of how percent wetness and number of wet patches were sampled; shown here are means for three measurements made in 1995.
** Numbers indicate size class of trees: 1 = 8<15 cm dbh; 2 = 15<23; 3 = 23<38; 4 = 38+ (no number indicates all size classes).
*** Coarse woody material (CWM) was measured in four size classes: 1 = 0<2 cm diameter; 2 = 2<5; 3 = 5<11; 4 = 11+ cm.

METHODS

I sampled abundance of wood frogs, and measured vegetation and wetness within 10 sampling sites in the Calling Lake research area. All 10 sampling sites were in continuous forest in 1993. In 1994, six sites became isolated fragments while four remained in continuous forest (i.e., control sites). Isolated fragments were created to investigate the effects of forest fragmentation on biodiversity; see Chapter III, Effect of Fragmentation on Wood Frogs (*Rana sylvatica*) in Boreal Mixedwood Forests. Sampling sites which were in fragments were not used in analyses to investigate habitat associations of wood frogs. Therefore, abundance data from all 10 sites in 1993 and from the four control sites in 1994 and 1995 were used.

Amphibians

Pitfall traps were used to collect information about wood frogs in the Calling Lake area. Pitfall trapping was selected as the most effective and efficient method of capturing wood frogs for three reasons: 1) my focus was on the terrestrial forested environment, not on breeding sites where other techniques are more appropriate; 2) abundance data were needed; and 3) sampling was repeated in the same sites over a three-year period. Pitfall traps were constructed and used for capturing wood frogs in the latter part of the 1993 field season, and throughout the summer of 1994 and 1995. Each of the sampling sites contained a sampling grid of 6 by 6 pitfall traps, covering an area of approximately 1.56 ha (125 by 125 m; Figure 2.1). The sampling grids were located centrally within each site to standardize edge effects when fragmentation occurred (see Chapter III).

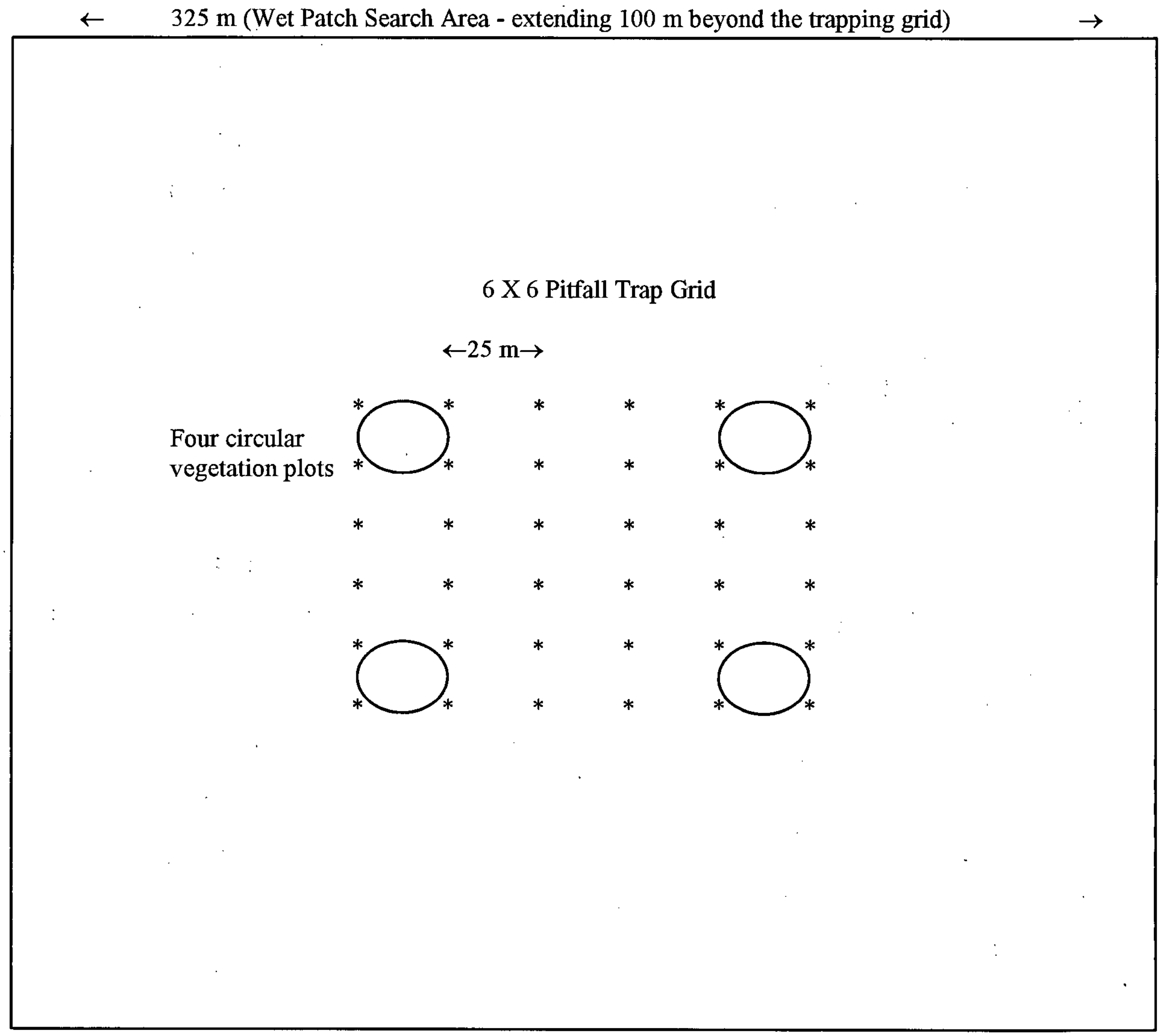


Figure 2.1. Layout of amphibian sampling sites, with trapping grid, four vegetation plots, and wet patch search area.

Pitfall traps were made by removing the bottom from a large coffee can and attaching it to another intact can with duct tape. Holes for water drainage were punched into the bottom of the intact can. A plastic collar (1 lb. margarine tub with bottom removed) was inserted on the top to keep frogs from escaping, and a plastic lid on the collar allowed traps to be closed when not in use. Within 2 m of a flagged point, a hole was dug slightly larger than the diameter of the cans, using a post hole auger. The cans were placed snugly into the hole, flush with the ground. A small amount of moss and/or debris was placed on the bottom of the trap to provide shelter and to maintain moisture. A slit was cut into the plastic collar and a cord was hung into the trap to allow small mammals (e.g., shrews) to climb out and escape. Pitfall traps were left open continuously and checked every two to three days. In 1993, the traps were opened as the construction of each grid was completed, and the sampling period differed for each of the 10 sites in that year. I therefore used the average number of frogs caught per day for comparison of wood frog abundance across different sites.

Information collected on each individual wood frog that I captured included the date, sampling site, trap number, mass (using a Pesola scale; visually estimated to within $\pm$ 0.1 g), body length (using calipers, visually estimated to within $\pm$ 0.5 mm; snout - urostyle with the frog pushed down slightly with the thumb to maintain consistency), and capture status (i.e., lack of toe clips indicated first capture, and a unique pattern of toe clips identified a recapture; see below). Size of individuals was recorded for two reasons: 1) to determine habitat associations of different size (age) classes ('new recruits' and 'adults'; see below); and 2) to eliminate 'new recruits' from capture data because they are quite transient and inclusion inflates abundance estimates in some areas (Heyer *et. al.*, 1994). I used length data to distinguish the different size (age) groups because I felt that it was measured more accurately in the field than mass (coefficient of variation around the sample mean was 23% - 28% for the length data from 1993 to 1995, and 73% - 85% for mass). Mass of individual frogs was likely affected more by duration of time spent in the trap than length due to exposure of individual frogs to different environmental conditions (e.g., length of time in the trap without food, bloating from sitting in flooded traps, etc.), and to measurement error (i.e., decreased precision of the 50 g Pesola scale at a low mass; many 'new recruits' were < 2 g).

I created three data sets: the first consisted of all size classes combined (referred to henceforth as the 'combined' data set); the second included only 'adults' (i.e., ≥ 25 mm); and the third included only 'new recruits' (i.e., < 25 mm). The term 'adult' does not necessarily represent breeding individuals, only those that were not 'new recruits'. The 'new recruits' data set represented very small individuals, comprised largely of newly metamorphosed frogs from that year. The size of the 'new recruits' was easily determined by an increase in captures of individuals at or near 25 mm in length during late summer (Figure 2.2) and from the literature (Bellis, 1961; 1965). Bellis (1965) found that new wood frog metamorphs, one week before emergence from their aquatic environment, were approximately 20 mm in length. He also noticed a surge in capture rate of young of the year in late July and early August, with metamorphs first captured between July 18 and August 4 (Julian dates 199 to 216), depending on the year.

Information on recapture rate and movements of wood frogs were obtained by marking and releasing trapped individuals (Ferner, 1979). I removed various toe tips using a marking system whereby each individual captured within a sampling site could be identified. The first individual caught within a site had the outer toe on the right hind foot clipped, the next

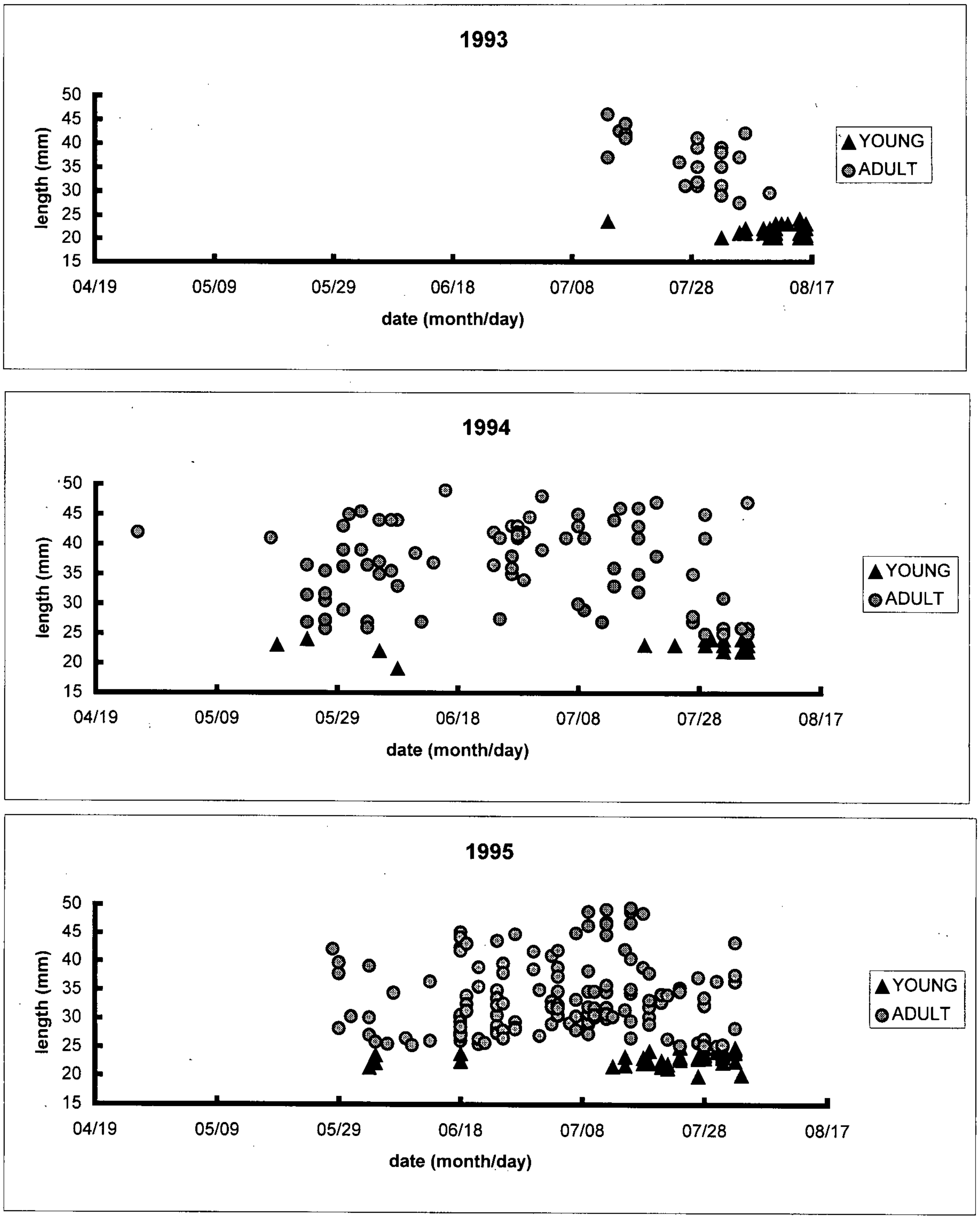


Figure 2.2. Body length of wood frogs (snout to end of urostyle), caught between 1993 to 1995. Some individuals caught early in the season that were < 25 cm were likely young from the previous year.

individual had the second outer-most toe clipped, and so on. After the first 10 individuals had been trapped and clipped in this manner the next nine individuals had their right, hind outer toe clipped plus one other. The marking of the hind feet alone, with only two toes clipped, allowed for identification of 54 individuals. If > 54 individuals were caught in one site in a given year then three hind toes were clipped. This system was repeated in each sampling site in each year. Some species of amphibians regenerate clipped toes; however, Berven (1990) claimed that wood frogs do not regenerate clipped toes, and Bellis (1965) recaptured marked individuals across years. In 1993, frogs were not marked but toe clipping was used in both 1994 and 1995.

Habitat and Vegetation

Habitat attributes of each sampling site were measured in four, 0.04-ha vegetation plots located at the corners of each sampling grid, among the outer four pitfall traps (Figure 2.1). Vegetation was sampled using circular plots, transect lines, and quadrats, and was generally consistent with the methods used by other studies in the Calling Lake area (Martin, 1992).

Two 22.6-m transects were placed at right angles in the centre of the vegetation plot. The ends of each transect defined the diameter of the largest circular plot. Within the largest circular plot (11.3-m radius), the number of trees of each species were counted and placed into one of four size classes (8 < 15, 15 < 23, 23 < 38, 38+ cm dbh). Within a smaller nested circular plot (5-m radius), the number of saplings and poles (< 8 cm dbh) of each tree species was counted. A 1-m^2 quadrat was placed at the centre of the circular plot and at the 5-m mark along each of 4 transect lines. In the centre quadrat, the number of stems of each shrub species (with stems taller than 50 cm) were counted. Within the remaining four quadrats percent ground cover was estimated visually to the nearest 5% for seven categories; all green vegetation, grasses/sedges, shrubs, forbs, leaf litter, woody material (all sizes), and mosses/ferns. Litter depth (cm) was measured at the 3-m mark along each transect line (i.e., four times per vegetation plot). Coarse woody material (CWM; all sizes) was measured along each transect line, and placed into four size classes (CWM1 = 0<2, CWM2 = 2<5, CWM3 = 5<11, CWM4 = 11+ cm diameter). Any piece of downed wood which crossed the transect line was included, and the diameter measured at the point of intersection.

Canopy closure was measured by ocular estimation within the four outer pitfall traps (i.e., overlaying the vegetation plot). A 40-cm long piece of PVC piping (2-cm diameter) was used to sight canopy closure directly above the researcher's head. A total of 30 points were distributed evenly between the four pitfall traps and recorded as either open or closed canopy, with open indicating that no foliage was in view, and partial or complete foliage cover classed as closed. The researcher walked systematically between the four traps following five transect lines (running north / south) placed 5 m apart, and measures were taken every 4 m along each line (six measures per line). A measure of canopy closure was then calculated by taking the ratio of closed sites to total sites measured and recorded as a percentage (e.g., 20 closed sites out of 30 sites equals 67% canopy closure).

Wet Patches

In 1994, wet patches were first located by walking systematically through the entire sampling site (325 by 325 m; Figure 2.1). Two researchers walked 25 m apart and noted the location of every 'wet' patch, which ranged from saturated soils (water appeared under foot pressure) to standing water, and the approximate size (area in m^2) of each patch was measured. The broad definition of wet patches was designed to include those which are wet only during part of the season. Wet patches retain water for different periods during spring and summer depending upon microsite (e.g., seep, depression, permanent, temporary, etc.).

Wet patches were first located and measured in late June to late July in 1994, which coincides with the wet season in north-central Alberta (Alberta Environmental Protection, 1996), and were re-measured at three times in 1995, in late April / early May, June, and July. The three repeated measures in 1995 provided a more accurate estimate of average wetness of each sampling site than did the single measure in 1994. The approximate size (area in m^2) of each wet patch was measured in the field and from this the percent wetness of the sampling site was derived (i.e., total area of all wet patches within each sampling site divided by the total search area, multiplied by 100). From these data, two independent variables were derived based on the mean from the three 1995 measures; percent wetness of the sampling site, and number of wet patches in the sampling site.

Different types of wet patches were observed in the field from broad microsite characteristics. To determine whether or not wood frogs were associating with different types of wet patches, six wet patch classifications were created based on two broad criteria. The first criteria, main vegetation component of the wet patch, had three classes; 1) the patch contained mostly trees throughout, with extensive canopy closure; 2) the patch contained mainly shrubs throughout, with few or no trees; and 3) the patch consisted of mainly grasses throughout, with no shrubs or trees. The second criteria, duration and extent of saturation, had two classes; 1) the patch was mainly dry all, or most, of the time; and 2) the patch was mainly wet all, or most, of the time.

Data Analyses

I conducted analyses on only those sites, and for periods, where fragmentation was not a confounding factor influencing amphibian abundance (i.e., all 10 sites in 1993, and the four control sites over the three-year sampling period). The four vegetation plots within each sampling site were analyzed separately to capture the greatest variability and detail in habitat attributes. These analyses were largely exploratory in nature, because the objectives were not proposed before the sampling design was established (improvements to the sampling design are mentioned in the discussion and in Chapter IV, Conclusions and Recommendations).

To investigate habitat associations of wood frogs in relation to terrestrial attributes (i.e., Objective 1), I used forward stepwise multiple regressions (SMR) and multivariate discriminant function analyses (MDA). I conducted a SMR on capture rates as a data reduction technique for control sites over the three sampling years. Using this technique for reduction ensures inclusion of all variables that are potentially biologically important in influencing abundance of wood frog (Myers, 1986). Assumptions for regression were likely not met due to the presence of numerous zeros in the data, therefore the SMR was used as a data reduction technique only and significance values for the model itself were ignored. I used data gathered from the 16 vegetation plots (4 control sites with 4 vegetation plots each) and the four pitfall traps immediately surrounding each plot. Only data from these four pitfall traps were used because they should reflect abundance of wood frogs within the vegetation plot more closely than data from the rest of the trapping grid. The total number of wood frogs caught over the three years within each group of four traps was the dependent variable. This was regressed against 51 independent habitat variables (see Appendix 1). If a variable was found in less than 25% of the vegetation plots it was excluded from the analyses for all plots. The stepping procedure was terminated when an insignificant variable entered the model (i.e., $\alpha > 0.05$).

Once independent variables were chosen by SMR, I conducted a series of MDAs to determine how well I could predict the presence or absence of wood frogs in 1993 based on these variables. I used only the pre-treatment 1993 data for the MDA to avoid any confounding effects of fragmentation, and to include a broader range of sites than those provided by only the control sites for 1994 and 1995. Capture rates in 1993 were relatively low when only four traps for each plot were used in the analysis, and the plots were easily assigned a present or absent value. The total number of captures per plot fell into four categories, with 28 plots having zero captures, and the remaining 12 plots containing one (n=9), two (n=1), or four (n=2) wood frogs. All plots in which frogs were captured were placed into the presence category, regardless of how many were caught, because the sampling period for each plot was uneven that year and the capture rates were low.

All of the chosen SMR variables were entered into a MDA together to determine how well the variables discriminated as a group. Each of the variables was then entered into a stepwise MDA (S-MDA) one at a time, in the order in which they were chosen by the SMR, to determine which subset of variables discriminated the best. Results from an MDA are always optimistic when the data used to derive discriminant functions are used to test the same data set, therefore, an N-way validation was done on half of the plots with the most significant discriminating variable (Tabachnick and Fidell, 1983). The four vegetation plots per sampling grid were used as groupings of the complete data set, and two groups of 10 plots were randomly selected for validation (i.e., vegetation plots 1 and 4). Each of the two groups was left out of the MDA, one at a time, and the remaining 30 plots were used to determine new discriminant functions, which the group of ten was then tested against. Once the variable list had been reduced and the most significant discriminating variable found from the MDA, a Pearson correlation analysis was conducted to determine which independent variables were correlated most highly with this discriminating variable. I repeated the SMR and MDA for the 'adult' data, then compared results from the two sets of analyses.

Pearson correlation analyses were conducted to investigate the relationship between the abundance of wood frogs and wetness of the sampling sites (i.e., Objective 2). The number of 'adult' and 'new recruits' caught in control sites in 1995 were used as dependent variables, and the average number of wet patches and the average percent wetness of control sites, based on the three sampling periods in 1995, were used as independent variables. I also examined the relationship between the density (i.e., number of each type) and the variety (i.e., number of different types) of wet patches to the abundance of wood frogs within control sites. A significance value of 0.10 was used for all statistical tests to reduce the probability of committing a Type II error, and all analyses were conducted with SYSTAT, Version 5 (Systat Inc., 1992).

RESULTS

Capture Rates

The capture and recapture rates of wood frogs in the Calling Lake area were quite low each year, especially in 1993, when sampling occurred for the shortest period (2 - 3 weeks; Table 2.2 shows capture rates of control sites). The rankings of the sites, in terms of high and

Table 2.2. Wood frog capture rates in control sites from 1993 to 1995 at Calling Lake, Alberta.

	1993	1994		1995			
Site	Mean No. Caught Per Day	Mean No. Caught Per Day	Recaptures	Mean No. Caught Per Day	Recaptures	Total Caught	Mean No. Caught Per Day
C - 1 Control	0.21 (0.00)*	0.18 (0.15)	0	0.23 (0.16)	0	34	0.21 (0.10)
C - 2 Control	0.07 (0.07)	0.10 (0.06)	0	0.25 (0.12)	0	26	0.14 (0.08)
C - 3 Control	0.06 (0.06)	0.11 (0.05)	0	0.38 (0.38)	1 (15 days apart)	36	0.18 (0.16)
C - 4 Control	0.06 (0.00)	0.07 (0.06)	0	0.38 (0.35)	2 (from 1994) 1 (21 days apart)	33	0.17 (0.14)
Mean	**0.10 (0.03)**	**0.12 (0.08)**		**0.31 (0.25)**			**0.18 (0.12)**

* data within brackets indicate 'adult' data set.

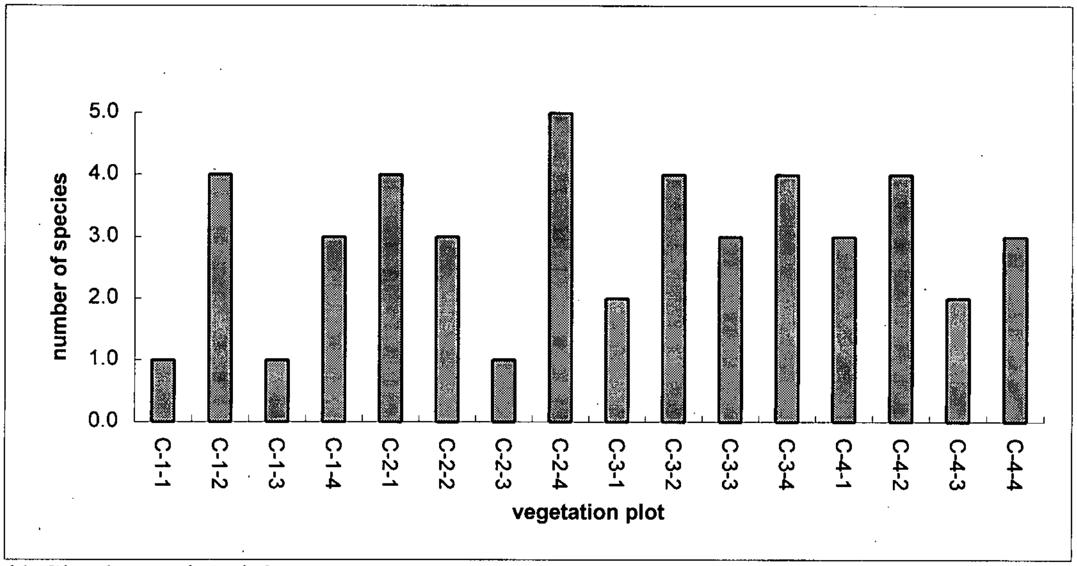
low capture rates, fluctuated from year to year. Recapture rates were too low for detecting trends across the sites. Among the four control sites for all three years combined, two had relatively higher capture rates of 'adults' compared to 'new recruits'; the other two sites had higher captures of 'new recruits' than 'adults'.

Habitat and Wet Patch Descriptions for Sampling Sites

The ten sampling sites were located within two different age classes of forest, as determined by Alberta Vegetation Inventory mapping (AVI). Sites T-1, H-1, C-1, and C-2 were in the younger age class (approximately 80 - 90 years old), and all other sites were within the older age class (approximately 110 - 130 years old). Vegetation plots within older control sites (i.e., C-3 and C-4) generally had higher tree and shrub species richness than did younger sites (Figure 2.3). Sites within these age classes also tended to differ in the density of trembling aspen (Figure 2.4); the younger sites had greater numbers of stems, especially in the first two size classes of trembling aspen, and the older sites generally had lower densities. The older sites also became more diverse in age class of trees, and they tended to have a greater mixedwood component, with increasing numbers of white spruce and paper birch entering into the subcanopy and canopy (Lee *et. al.*, 1995). The older sites had higher shrub densities, with shrubs often reaching > 1.5 m in height, as well as the presence of numerous gaps in the tree canopy. Furthermore, the younger sites tended to be relatively dry compared to the older sites, which were split between being either very wet (Sites T-2, H-2, C-3, and C-4), or relatively dry (Sites T-3 and H-3; Figure 2.5).

Percent wetness ranged from 0 - 12% across the sites in 1994, and from 0 - 20% among the three sampling periods in 1995. A comparison of the 1994 results to the last two samples in 1995 (overlapping periods for both years) indicated that all but two sites (Sites T-2 and C-3)

a) Tree species richness



b) Shrub species richness

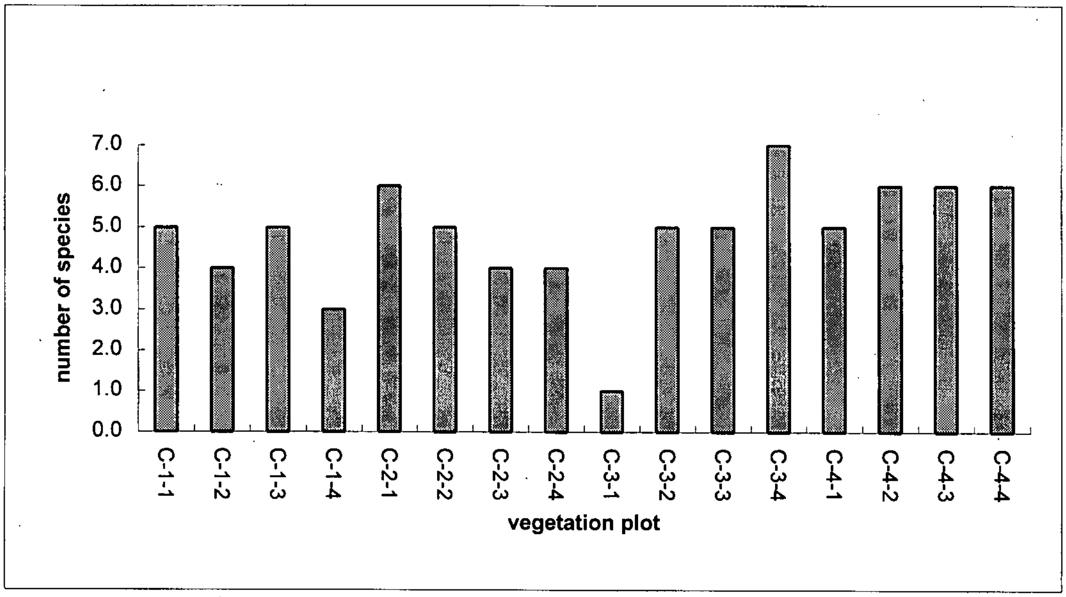


Figure 2.3. Tree and shrub species richness (i.e., number of different species of each) within each vegetation plot in control sites.

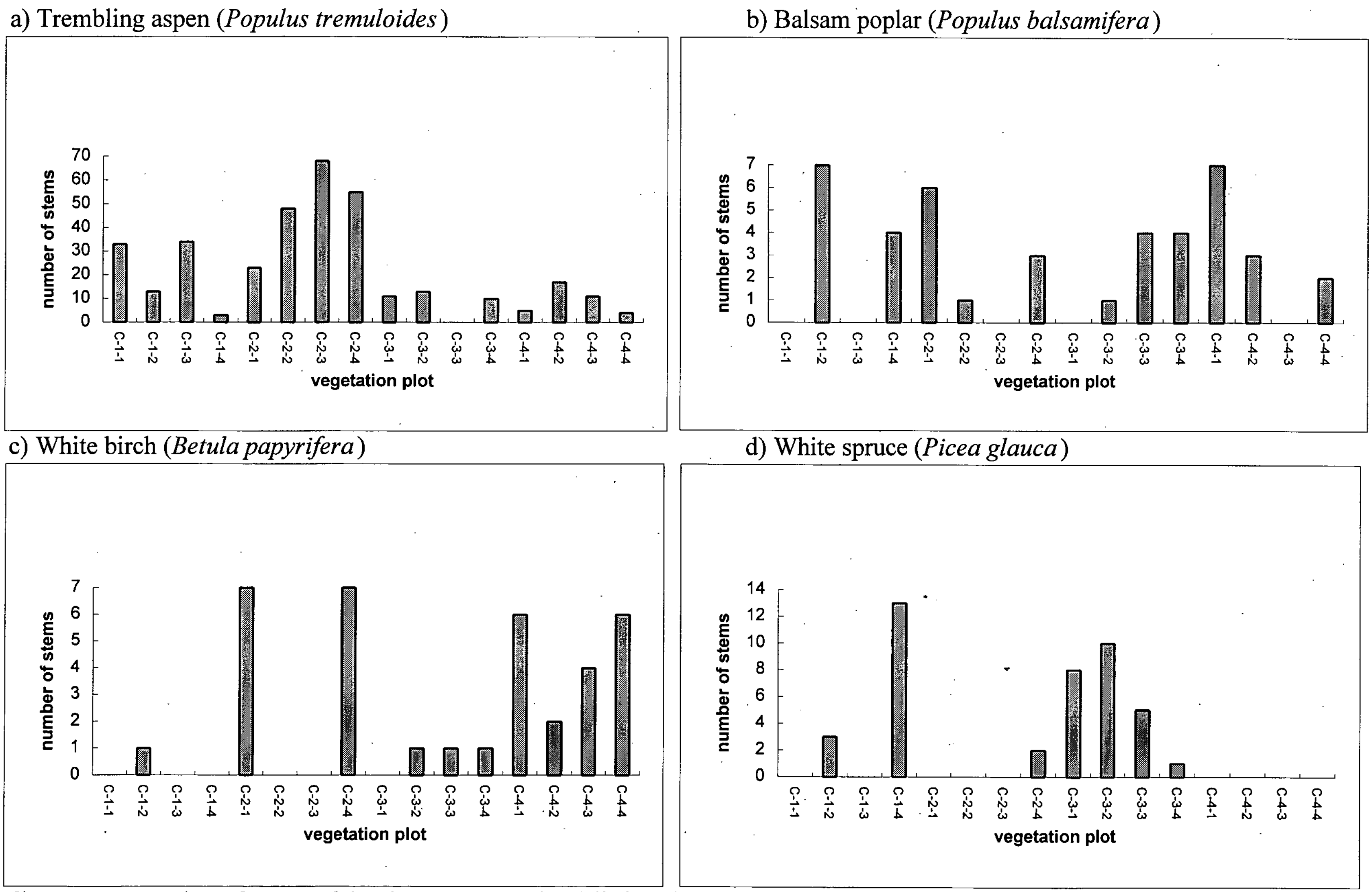
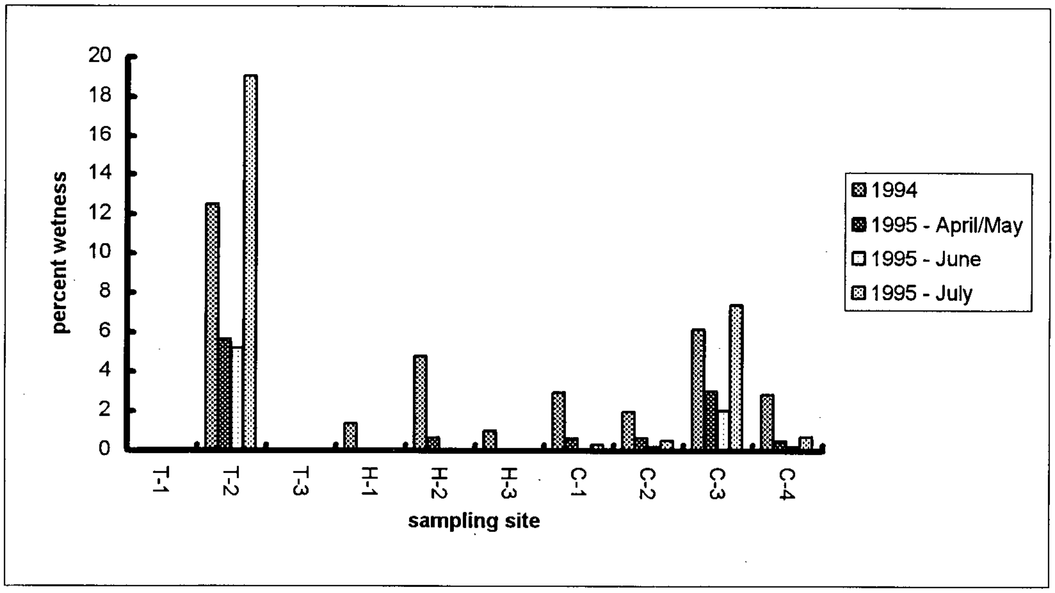


Figure 2.4. Number of stems of dominant tree species (all size classes combined) within four vegetation plots in control sites. Note: Scales on the y axes differ to highlight the variability across plots, rather than that between species.



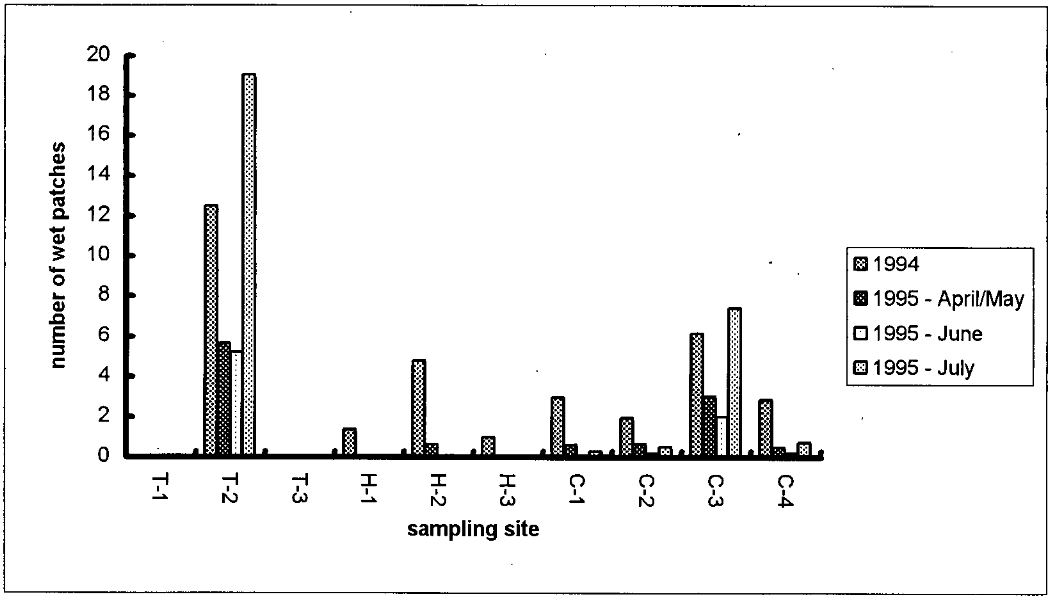


Figure 2.5. Percent wetness and number of wet patches within each sampling site in 1994 and 1995.

were drier in 1995 than 1994. A site which ranked high for one wetness variable did not necessarily rank high for the other variable. For example, site T-2 ranked much higher for percent wetness than any other site but was lower in terms of number of wet patches, reflecting fewer and larger wet patches compared to those at other sites.

Size of the wet patch and water depth were highly variable during the field season. In general, wet patches appeared to fall into two broad categories: those which appeared to be seeps and were ground fed or stream fed, and those which were more like depressions, collecting snowmelt and precipitation. Those which appeared to be ground or stream fed tended to be quite long, and it was difficult to tell where one wet patch ended and another began. Each wet patch tended to be dominated throughout by either grasses and sedges, shrubs, or trees. Some wet patches changed quite substantially over the field season in terms of their overall wetness, however, the seepages appeared to change the least, or at a slower rate, than those classed as depressions.

Habitat Associations of Wood Frogs

Variables are defined in Appendix 1 and results from the SMR on the 'combined' data set are summarized in Table 2.3. The stepping procedure was completed after five steps, because the sixth step included a non-significant variable. The variables have been placed in the order that they were chosen in the stepping procedure, and the coefficient signs indicate a positive or negative relationship. Results from the MDA with all five chosen SMR variables indicated an 80% correct classification of the 40 presence / absence plots in 1993 (Table 2.4a). A S-MDA with the first variable, and S-MDA with the first two variables, chosen from the SMR (i.e., SHRUBRICH and GRASS/SEDGE) each resulted in a 60% correct classification of the 1993

Table 2.3. Forward stepwise multiple regression (SMR) of total number of wood frogs caught between 1993 and 1995 in 16 vegetation plots within control sites. (Note: results used only for data reduction).

Variable chosen; in order of appearance	Coefficient sign
Shrub species richness* (SHRUBRICH)**	-
% ground cover of grasses and sedges (GRASS/SEDGE)	+
Coarse woody material (5<11 cm diameter) (CWM3)	+
White spruce (23<38 cm dbh) (PIC3)	+
Trembling aspen (38+ cm dbh) (TREM4)	+

* Number of different shrub species found within the plot.
** Variable codes defined in Appendix 1.

Table 2.4. Multivariate discriminant function analysis (MDA) for all frogs captured during the 1993 pre-treatment year, with sites classified as present or absent. Variables used for discrimination were those selected from a stepwise multiple regression (SMR) with all size classes of frogs combined within control sites from 1993 to 1995. See Appendix 1 for definitions of variables.

a) Classification table for MDA with 40 plots using all 5 SMR variables entered at once.

	Predicted Classification			
	Category (1993)	Absent	Present	Total
Correct Classification	Absent	**23***	5	28
	Present	3	**9***	12
	Total	26	14	**40**

Percent correctly classified = **80%**

* 23 of 28 plots, and 9 of 12 plots, were correctly classified as present or absent respectively.

b) Percentage of plots correctly classified as present or absent using a stepwise MDA and 5 SMR variables. Variables were entered in the order which they appeared in the SMR.

Variable	Percent of Plots Correctly Classified
SHRUBRICH	60%
+* GRASS/SEDGE	60%
+ CWM3**	80%
+ PIC3	80%
+ TREM4	80%

* '+' indicates the addition of that variable into the analysis with all other variables shown above.
** The mean value for this variable is significantly different between plots classified as either present or absent in 1993 ($P < 0.001$).

c) Classification table for MDA with significant variable CWM3 and 40 plots from the 1993 data set; including N-way validation of 20 plots.

	Predicted Classification			
	40 Plots in 1993	Absent	Present	Total
Correct Classification	Absent	**21***	7	28
	Present	2	**10***	12
	Total	23	17	**40**
	Percent correctly classified = **78%**			
	N-way Valid. on 20 Plots	Absent	Present	Total
Correct Classification	Absent	**9**	5	14
	Present	1	**5**	6
	Total	10	10	**20**
	Percent correctly classified = **70%**			

* 21 of 28 plots, and 10 of 12 plots, were correctly classified as present or absent respectively.

data set. A S-MDA with the first three variables (i.e., including CWM3) resulted in an 80% correct classification (Table 2.4b). This value did not increase with the addition of the fourth and fifth variables (i.e., PIC3 and TREM4). Results from univariate F-tests indicated that only the mean value for CWM3 was significantly different between plots categorized as present or absent ($P < 0.001$). The results from a MDA with CWM3 alone indicated a 78% correct classification of the 1993 plots; an N-way validation provided a more accurate assessment of discrimination ability (70%; Table 2.4c).

The results from the 'adult' SMR and S-MDA are presented in Tables 2.5 and 2.6. Results from the 'combined' and 'adult' data sets were quite similar; CWM3 was again chosen in the 'adult' SMR, and its mean value, along with the mean value for %FORBS, was significantly different between plots categorized as either present or absent ($P = 0.03$ and 0.04 respectively; Table 2.6b). The addition of CWM3 to the multi-discriminant model increased prediction accuracy by 15-20% for both data sets. Using both significant SMR variables from the 'adult' data set (i.e., CWM3 and %FORBS) did not improve the prediction accuracy beyond that obtained with CWM3 alone (i.e., 73% correct classification versus 78% respectively). The prediction accuracy of the MDAs for both data sets were identical when all SMR variables were included (i.e., 80% correct classification).

A Pearson correlation analysis of all variables within all 40 vegetation plots indicated that CWM3 was positively correlated with trembling aspen (15<23 cm dbh; $P = 0.09$, $r = 0.44$), and negatively correlated with tree species richness (all size classes combined; $P = 0.03$, $r = -0.54$), tree species richness of size class 15<23 cm dbh ($P = 0.04$, $r = -0.51$), and number of stems of balsam poplar (all size classes combined; $P = 0.04$, $r = -0.51$).

Table 2.5. Forward stepwise multiple regression (SMR) of 'adult' wood frogs caught between 1993 and 1995 in 16 vegetation plots within control sites. (Note: results used only for data reduction).

Variable Chosen; in order of appearance	Coefficient sign
Shrub species richness (SHRUBRICH)*	-
Snowberry shrubs (SNOW)	-
Coarse woody material (5<11 cm diameter) (CWM3)	+
% ground cover of forbs (FORBS)	-
White spruce (all sizes combined) (PICALL))	-
White spruce (23<38 cm dbh) (PIC3)	+
Balsam poplar (15<23 cm dbh) (BAL2)	+

* Variable codes defined in Appendix 1.

Table 2.6. Multivariate discriminant function analysis (MDA) for all frogs captured during the 1993 pre-treatment year, with sites classified as present or absent. Variables used for discrimination were those selected from a stepwise multiple regression (SMR) with 'adult' wood frogs within control sites from 1993 to 1995. See Appendix 1 for definitions of variables.

a) Classification table for MDA with 40 plots and all 7 'adult' SMR variables entered at once.

		Predicted Classification		
	1993 - 'Adult' Data Set	Absent	Present	Total
Correct Classification	Absent	**27***	6	33
	Present	2	**5**	7
	Total	29	11	**40**

Percent correctly classified = **80%**

* 27 of 33 plots, and 5 of 7 plots, were correctly classified as present or absent respectively.

b) Percentage of plots correctly classified as present or absent using a stepwise MDA and 7 'adult' SMR variables. Variables were entered in the order that they appeared in the SMR.

Variable	Percent Correctly Classified
SHRUBRICH	60%
+ SNOW	65%
+ CWM3*	80%
+ FORBS*	80%
+ PICALL	80%
+ PIC3	80%
+ BAL2	80%

* The mean value for this variable is significantly different between plots classified as present or absent in 1993 (CWM3, $P < 0.001$; and %FORBS, $P = 0.023$).

c) Classification table for MDA with 2 significant 'adult' SMR variables only (i.e., CWM3 and FORBS).

		Predicted Classification		
	1993 Data Set	Absent	Present	Total
Correct Classification	Absent	**24***	9	33
	Present	2	**5**	7
	Total	26	14	**40**

Percent correctly classified = **73%**

* 24 of 33 plots, and 5 of 7 plots, were correctly classified as present or absent respectively.

Wet Patches and Abundance of Wood Frogs

In control sites during 1995, the abundance of 'adult' wood frogs was positively correlated with both the number of wet patches and variety of wet patches found within a site (i.e., number of different types of wet patches; Table 2.7). Four of the six wet patch categories occurred within control sites. In 1995, there were significant, but opposing, correlations found for the 'adults' and 'new recruits' in terms of their association with the variety of wet patches; for the 'adults' it was positive ($P = 0.05$, $r = 0.95$), and for the 'new recruits' it was negative ($P = 0.02$, $r = -0.98$).

DISCUSSION

Wood frogs in the Calling Lake area appear to be associated with some aspects of the terrestrial environment, in particular the abundance of coarse woody material (5<11 cm diameter; CWM3), and hence the age class or community type where CWM3 is prevalent. For example, CWM3 was most closely associated with aspen trees of approximately 15<23 cm dbh. Aspen of this size (age) class may be the dominant tree species in a community type which provides a host of other habitat attributes (e.g., appropriate soil moisture and pH, humidity levels, prey, etc.) that wood frogs may require but were not measured in this study. Given the nature of the sampling design (i.e., it was not established to address habitat association questions and there were relatively few sites and observations), the strong relationship found between abundance of wood frogs and CWM3 was not expected.

Table 2.7. Significant Pearson correlation analysis results between the wetness of the site and wood frog relative abundance in 1995.

Variable - 1995	'Adult' Wood Frogs		'New Recruits'	
	r	P	r	P
Average number of wet patches	0.92	0.09	-	-
Variety* of wet patches	0.95	0.05	-0.98	0.02

* Variety is defined here as the number of different types of wet patches found within a sampling site.

Other amphibian habitat association studies indicate that vegetation variables and forest age are poor predictors of diversity or abundance of amphibians, and that habitat structure and physiographic gradients are better predictors (Aubry and Hall, 1991; Bury *et. al.*, 1991; Gilbert and Allwine, 1991; Morrison *et. al.*, 1995). McAlpine and Dilworth (1989) found that structural aspects of habitat, principally those associated with vegetation (i.e., density of vegetation and tree canopy, and proximity to standing water), were the most important factors in differentiating locations of species. In the Calling Lake area, decreased species richness of shrubs, decreased percent ground cover of forbs, increased percent ground cover of grasses/sedges, and particularly increased amounts of mid to large sized coarse woody material, were identified as potential structural attributes that may influence the presence and abundance of wood frogs. Examples of other structural attributes which may be important for amphibians, but were not measured or included in the analyses, are structural complexity of vegetation measured at various heights, and the diversity of tree size classes (i.e., the standard deviation of dbh). Coarse woody material (CWM) has been identified as a key habitat attribute for many terrestrial amphibians, particularly members of the *Plethodontidae* (Jaeger, 1980; Dupuis *et. al.*, 1995). In the Cascade Range of Washington, the red-legged frog (*Rana aurora*) appears to associate with CWM that is characteristic of old-growth forests and unmanaged young stands (Aubry and Hall, 1991). Amphibians use CWM both for shelter from harsh climatic conditions and cover from predators, as well as potential breeding sites. Interstitial spaces between CWM, rocks, moss cover, leaf litter and the soil surface provide a relatively constant environment in terms of temperatures and moisture levels, that is ideal for amphibians (Heatwole, 1962; Jaeger, 1980; Welsh, 1990).

There appears to be a positive relationship between the number and variety of wet patches found within an area and the abundance of 'adult' wood frogs. However, only four control sites and data from one year were used for these analyses. When the fragmented sites are considered as well, many of the driest sites, with few if any wet patches, had some of the highest capture rates (i.e., Site H-1 for all three years, and sites T-1 and T-3 in 1993). These anomalies make it difficult to interpret my results, indicating that climatic variability from year to year may influence wood frog associations with standing water in any given year, and that long term, large scale, studies are needed.

Wood frogs appear to demonstrate varying degrees of association with standing water among different geographic locations. In northern Minnesota, Bellis (1965) found summer home ranges were at least 450 m from the nearest pond, whereas in southern Michigan, Heatwole (1961) found greater densities of wood frogs in areas where there were numerous ponds. A study conducted in the eastern part of Alberta's boreal forest in 1976 and 1977 (Roberts and Lewin, 1979) was centered around the habitat associations of three amphibian species within 100 m of pond edges. They found that all three species were close to water, with the wood frog usually found within 20 - 60 m, and rarely at a distance of 100 m, from the shoreline. In Calling Lake, Alberta, I found that sites which were consistently high in terms of abundance of wood frogs (e.g., Site H-1) were those which were relatively dry, where the closest wet area was more than 100 m from the sampling grid, and likely closer to 200 - 500 m away. Roberts and Lewin's study was conducted in a relatively dry part of Alberta, where the soils are sandy, and jack pine is often the dominant tree species (Rowe, 1972). Their study area differs from more central parts of the boreal forest in Alberta, like the Calling Lake area, where aspen / poplar and white spruce are the dominant species. These mixedwood communities occur on relatively mesic sites (Corns and Annas, 1986). Wood frog populations in eastern Alberta may have adapted to drier regions by remaining closely associated with standing water.

Amphibians depend upon moisture and standing water for gas exchange, rehydration and for breeding (Adolph, 1932), but they have varying degrees of association with soil moisture depending upon the species, geographic location, and season. A study conducted in New York found high variability among different species regarding their associations with soil moisture and pH, and moist quadrats had significantly more wood frogs compared to dry quadrats (Wyman, 1988). However, in the Cascade Range of Washington, Aubry and Hall (1991) found decreased species richness with increased stand moisture. They concluded that wet old-growth stands provided low-quality habitat for several species (e.g., *Ensatina eschscholtzii* and *Taricha granulosa*), including the red-legged frog, which reached its highest abundance in moderately moist sites. In the Cascade Range of Oregon, most amphibians were collected from mesic sites, and geographic locations with the least amount of rainfall had reduced numbers of amphibians and a greater selection for mesic-wet stands over dry stands (Gilbert and Allwine, 1991). In California, Harris (1975) found that *Hyla cadaverina* moved to water in summer, when conditions are most dry and hot, and away from water in winter, locating themselves in deep rock crevices. Contrasts in association with soil moisture and standing water across geographic locations may relate to differences in climatic, elevational, topographical, and temporal gradients. In areas with greater precipitation, higher humidity, lower topography, or higher clay content in the soils, the soil and organic matter may retain moisture longer, and amphibians may be less dependent on standing water to avoid desiccation. In such areas, aspects of the terrestrial environment which retain moisture (e.g., rocks, logs, moss cover, etc.) may be very important to amphibians. This adaptability and expansion into terrestrial environments makes amphibian habitat associations less predictable.

Many pond breeding amphibians breed in ephemeral pools that are undetectable by aerial photography, and the protection of these breeding sites is essential for preserving stable amphibian populations. Berven (1995) found that the size of the adult wood frog population in three different geographic locations was related closely to juvenile recruitment, which in Alberta, may depend on amount of winter snowmelt. Winters in the north are long and cold, with variable amounts of snowpack among years. Wood frogs breed in early spring (i.e., mid-April to May), and their choice of breeding locations may depend upon snow deposition and spring runoff. The average winter precipitation (Oct. - Mar.) for Calling Lake, from 1961 - 1990, was 120.4 mm. In 1994, it was 178.7 mm, and in 1995 it was only 80.3 mm (Alberta Environmental Protection, 1996). In 1995, the first wet patch search revealed that very few of the wet patches located in late summer 1994 contained sufficient standing water for egg laying. The fact that the wet patches were quite dry by late April, and drier still in June, may indicate a possible breeding limitation imposed on wood frogs in some years. The wetness of a site appears to generally increase by late summer (July / August), but if the wetness of an area were only measured at that one time, the number of wet patches may be inflated from those available in the breeding season, skewing estimates of potential breeding sites. Managers must be aware that not all sites which are wet in late summer are possible breeding sites in early spring, and that not all wet patches are used by all amphibian species for breeding. Richter and Azous (1995), in the Puget Sound area, found that species richness and diversity were not related to size of wetland, and they indicate that size of the breeding population likely reflects favourable breeding habitat rather than overall wetland size. They also stress the importance of acknowledging smaller wetlands as important habitat for amphibians. In the Calling Lake area, some of the larger seepages which remained wet throughout the summer can be found on AVI maps used by the forest industry. These areas are likely to be the first areas which would be considered for protection as amphibian habitat, in part due to their low timber value. However, these seepage areas were less common across the study area than depressions that retain water, and it is unknown if seeps are suitable breeding habitat for amphibians. If the number of wet patches is an important factor in wood frog population dynamics, then the large number of depressions, which serve as ephemeral breeding sites in years with high snow melt, and wet springs, which are available when the ground is still frozen, will be left unprotected under current management guidelines.

Protection of wood frog habitat in the boreal mixedwood forest of Alberta requires more detailed investigations into habitat use during the breeding season, summer months, and for hibernation. Wood frogs appear to be associating with aspects of habitat at the stand level (i.e., CWM) during summer, but the extent of that association cannot be discerned from my research. In concert with determining stand level associations of amphibians, research should be expanded to the landscape level, to determine the relative importance of various habitat types found within the ecoregion. Each potential habitat type within this ecosystem (i.e., coniferous, deciduous, mixedwood, etc.) should be identified, with subsequent sampling for each cohort group at different times of the year within each habitat. Movement patterns between hibernation sites, breeding sites and summer home ranges in relation to habitat type should be investigated, especially in the face of broadscale landscape level changes that forest harvesting will have on these movements. In addition, the utility of different types of wet patches as breeding sites should be determined and potential source areas for local populations should be identified (Pulliam, 1988).

CHAPTER III

EFFECT OF FRAGMENTATION ON WOOD FROGS (*RANA SYLVATICA*) IN BOREAL MIXEDWOOD FORESTS

INTRODUCTION

Effects of forestry on amphibians have been studied in numerous parts of North America. Species diversity and relative abundance of some amphibian species are reduced in clearcuts and second-growth stands compared to old-growth forests (Welsh 1990; Petranka *et. al.* 1994; Dupuis *et. al.* 1995). Explanations for these trends include the inhospitable micro-climate created by the removal of forest cover, and decreased amounts of large, woody material on the ground in harvested areas and second-growth stands (Jaeger 1980; Aubry *et. al.* 1988; Welsh 1990). Increased temperature, wind, and UV radiation are incompatible with the unique physiological characteristics of an amphibian's skin, and downed wood provides protective cover to many salamander species. Amphibians require moisture to facilitate gas exchange and they are ectothermic. Therefore, they are constrained to living in relatively stable environments with moist conditions like those found within forests (Heatwole, 1962; Zug, 1993).

One of the major concerns associated with forest harvesting is that of habitat fragmentation. Because of the relationship between species richness and size of oceanic islands, where the equilibrium theory of island biogeography (MacArthur and Wilson, 1967) was first hypothesized, ecologists predict that as a forested area becomes fragmented, patches of isolated habitat will experience decreased species richness through time. Decreased relative abundance within isolated forest fragments is one potential demographic response a population may exhibit in a newly fragmented area, that may eventually lead to local extirpation. Decreased species richness and relative abundance within fragments may be related to isolation, edge effects and density-dependent factors (Lovejoy *et. al.*, 1986; Harris and Silva-Lopez, 1992). Amphibians, like many species, may be susceptible to impacts of fragmentation. Many pond breeding amphibian species migrate to and from breeding sites annually, and clearcuts may pose barriers to these movements. Edges, like those created by clearcuts, may have increased temperatures, wind speeds, and UV exposure (Lovejoy *et. al.*, 1986), all of which make environmental conditions more extreme and unsuitable for amphibians and their larvae. Edges may also have increased predation risks (Andren and Angelstam, 1988; Harris and Silva-Lopez, 1992). To my knowledge, potential impacts resulting from creation of isolated forest fragments have not been tested for amphibian populations in temperate and boreal forests; however, studies have been conducted in the Central Amazonian rainforests (Zimmerman and Bierregaard, 1986; Gascon, 1993).

At Calling Lake, Alberta, a large collaborative study was initiated to determine the impacts of fragmentation and forest harvesting on biodiversity in boreal mixedwood forests (Schmiegelow and Hannon, 1993). The effects that forest harvesting will have on wildlife within this ecosystem are not well known (Dancik *et. al.* 1990). The study is investigating potential impacts of harvesting on various taxonomic groups, including birds, small mammals, and amphibians. My thesis focused on the wood frog (*Rana sylvatica*), which is an ideal amphibian species for addressing fragmentation effects because of its relatively long migrations to and from breeding and hibernation sites (Bellis, 1965), extensive use of the terrestrial environment (Bellis, 1962), relatively high abundance in the area, and greater trappability than the other two amphibian species found in the Calling Lake area. The objective of this chapter is to investigate effects of fragmentation on wood frogs in boreal mixedwood forests.

METHODS

Amphibians

Effect of fragment size on wood frogs was addressed by pitfall trapping in three 10-ha fragments, three 100-ha fragments, and four control sites. Pitfall trapping was conducted in the Calling Lake area each summer between 1993 and 1995. See Chapter II, Habitat Associations of Wood Frogs (*Rana sylvatica*) in Boreal Mixedwood Forests, for details regarding the layout of the sampling site, the sampling period, construction of pitfall traps, and information collected on each individual caught.

Data Analyses

I analyzed both capture and body length data to evaluate effects of fragmentation on wood frog populations. Analyses of the capture data were conducted on the 'combined' data set, as well as the 'adult' data set. The length data were analyzed for the 'combined' data set only. A repeated measures analysis of variance (RM-ANOVA) was used for all data sets, with captures of wood frogs in the two post-harvest years (i.e., 1994 and 1995) serving as repeated measures. The change in capture rate and average body length for the first and second year after harvesting were the dependent variables (i.e., the difference between 1993 and 1994 results, and the difference between 1993 and 1995 results). Analyses were conducted on the differences in capture rate and length data across years to include the pre-treatment data (i.e., 1993) as a standard against which to compare the two post-harvest years and to control for between site variation. A significance level of 0.10 was used for all analyses to reduce the probability of committing a Type II error, and all analyses were conducted with SYSTAT, Version 5 (Systat Inc., 1992).

RESULTS

Capture Rates

Capture and recapture rates of wood frogs were low in the Calling Lake area, especially for 'adults', and for many sites these rates fluctuated greatly among years (Table 3.1). Some individuals marked in 1994 were recaptured in 1995; however, there were no apparent trends in recapture rates and locations among the different treatments.

Capture rates were highly variable, both within a site between years, as well as between sites within and between treatments (Figure 3.1). For the 'combined' data set, capture rates within the three 10-ha fragments responded differently in 1994, but all sites showed decreased abundance of wood frogs in 1995 (second year post-harvest) compared to 1993 (pre-harvest year). Capture rates in the 100-ha fragments followed a consistent 'V-shaped' pattern for both data sets, with 1994 having the lowest capture rates and 1995 having the highest. As a group, the 100-ha sites had the greatest variability in capture rates over the three years because they included sites of highest and lowest abundance (i.e., Sites H-2 and H-3 respectively). Trends

Table 3.1. Wood frog (*Rana sylvatica*) capture rates for forest fragments and control sites, between 1993 and 1995 at Calling Lake, Alberta.

	1993	1994		1995			
Site	Mean No. Caught Per Day	Mean No. Caught Per Day	Recaptures	Mean No. Caught Per Day	Recaptures	Total Caught	Mean No. Caught Per Day
T - 1 10-ha	0.18 (0.14)*	0.27 (0.23)	2 (same individual; 9 & 13 days apart) 1 (21 days apart)	0.10 (0.09)	1 (from 1994)	33	0.18 (0.15)
T - 2 10-ha	0.40 (0.08)	0.11 (0.10)	0	0.23 (0.22)	1 (from 1994) 1 (unclear)	35	0.25 (0.13)
T - 3 10-ha	0.35 (0.12)	0.12 (0.11)	0	0.01 (0.01)	0	20	0.16 (0.08)
Mean	**0.31** **(0.19)**	**0.17** **(0.15)**		**0.11** **(0.11)**			**0.20** **(0.12)**
H - 1 100-ha	0.67 (0.48)	0.39 (0.18)	0	0.83 (0.49)	3 (from 1994)	103	0.63 (0.38)
H - 2 100-ha	0.24 (0.18)	0.08 (0.06)	0	0.29 (0.16)	1 (15 days apart)	31	0.20 (0.13)
H - 3 100-ha	0.08 (0.00)	0.02 (0.02)	0	0.10 (0.09)	1 (9 days apart)	11	0.07 (0.04)
Mean	**0.33** **(0.22)**	**0.16** **(0.09)**		**0.41** **(0.25)**			**0.30** **(0.18)**
C - 1 Control	0.21 (0.00)	0.18 (0.15)	0	0.23 (0.16)	0	34	0.21 (0.10)
C - 2 Control	0.07 (0.07)	0.10 (0.06)	0	0.25 (0.12)	0	26	0.14 (0.08)
C - 3 Control	0.06 (0.06)	0.11 (0.05)	0	0.38 (0.38)	1 (15 days apart)	36	0.18 (0.16)
C - 4 Control	0.06 (0.00)	0.07 (0.06)	0	0.38 (0.35)	2 (from 1994) 1 (21 days apart)	33	0.17 (0.14)
Mean	**0.10** **(0.03)**	**0.12** **(0.08)**		**0.31** **(0.25)**			**0.18** **(0.12)**
All sites	0.23 (0.11)	0.15 (0.10)		0.28 (0.21)		362	0.38 (0.14)

*data within brackets indicate 'adult' data set.

a) 'Combined' data set   b) 'Adult' data set

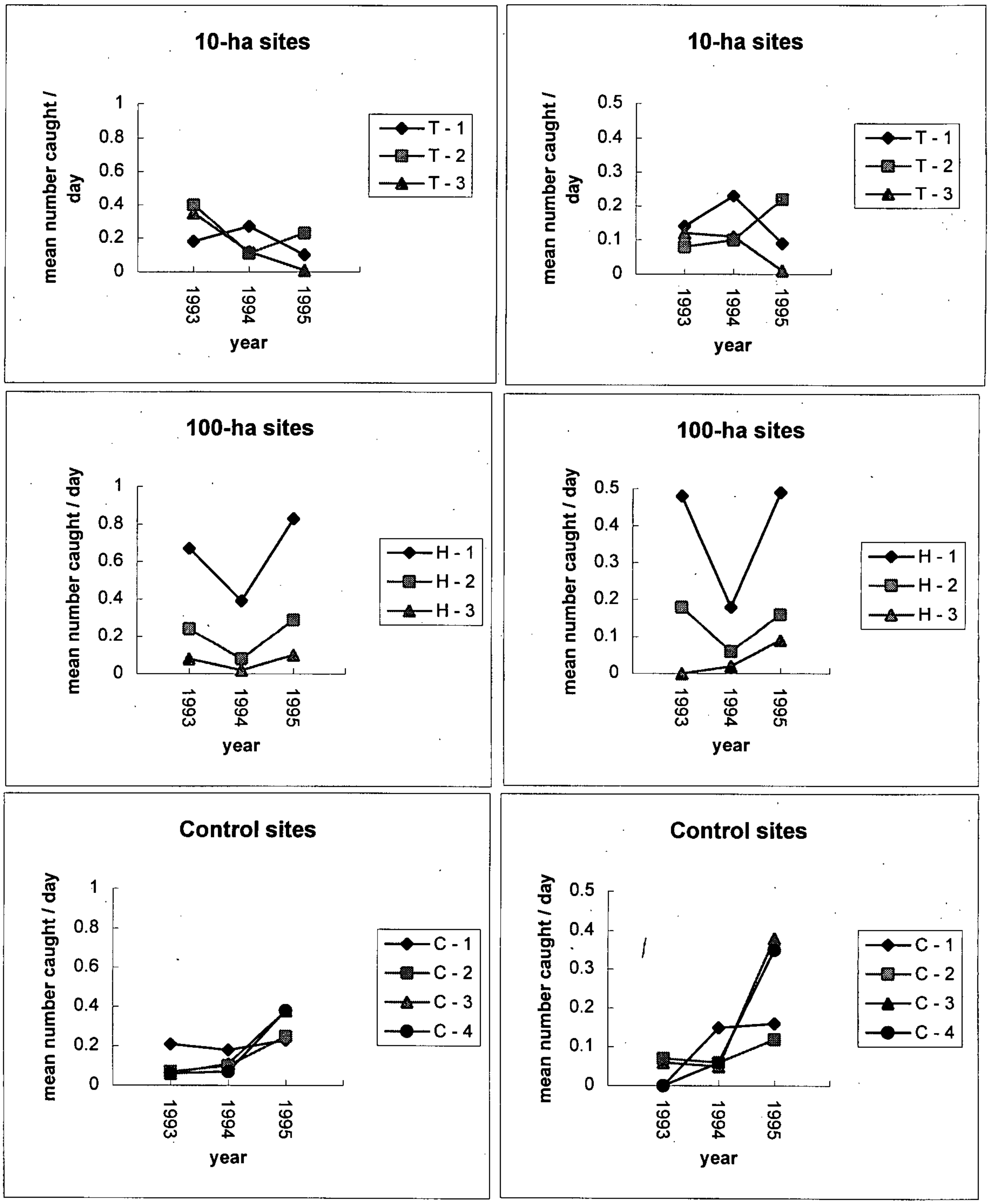


Figure 3.1. Capture rate of wood frogs by site and treatment at Calling Lake Alberta, 1993-1995. Scales on y-axes for 'combined' and 'adults' differ.

within the control sites were more variable than trends within the 100-ha fragments, but all control sites had consistently higher capture rates in 1995 than in 1993 and 1994.

The highest capture rates of 'adult' wood frogs during the pre-harvest year occurred at two of the 10-ha fragments (i.e., Sites T-1 and T-3) and two of the 100-ha fragments (i.e., Sites H-1 and H-2). The same two 10-ha fragments had the lowest capture rates the second year after harvesting (i.e., 1995), although this year had the highest capture rates of 'adults' for six of the ten sites.

Treatment Effects

The RM-ANOVA for the change in wood frog capture rate was significant for the 'combined' data set (Table 3.2). A significant year by treatment interaction for the wood frog capture data indicated that the treatments had a different effect on wood frog capture rates through time (P = 0.09). The 100-ha and control sites followed similar upward trends (i.e., increased capture rates from the first post-harvest year to the second), whereas the 10-ha sites followed an opposite trend (i.e., decreased capture rates two years post-harvest; Figure 3.2). The RM-ANOVA for the 'adult' data set indicated a significant year and treatment effect (P = 0.06 and P = 0.08 respectively; Table 3.3). Similar trends were found for the 'adults' as for the 'combined' data set in terms of a potential interaction between year and treatment, although it was not significant (P = 0.19; Figure 3.3).

A significant interaction between treatment and year was found for the change in mean body length of all size classes of wood frogs combined among treatments (Table 3.4; P = 0.07). In addition to decreased capture rates, wood frogs in the three 10-ha fragments had an increased mean length of captured individuals two years after harvesting compared to the 100-ha and

Table 3.2. Repeated measures analysis of variance (RM-ANOVA) comparing the change in capture rate of wood frogs ('combined' data set) between the first and second year after harvesting among different treatments.

Between Treatments					
Source	SS	DF	MS	F	P
Treatment	0.28	2	0.14	6.95	0.02
Error	0.14	7	0.02		
Within Treatments					
Source	SS	DF	MS	F	P
Year Effect	0.08	1	0.08	7.29	0.03
Treatment by Year	0.08	2	0.04	3.52	0.09
Error	0.08	7	0.01		

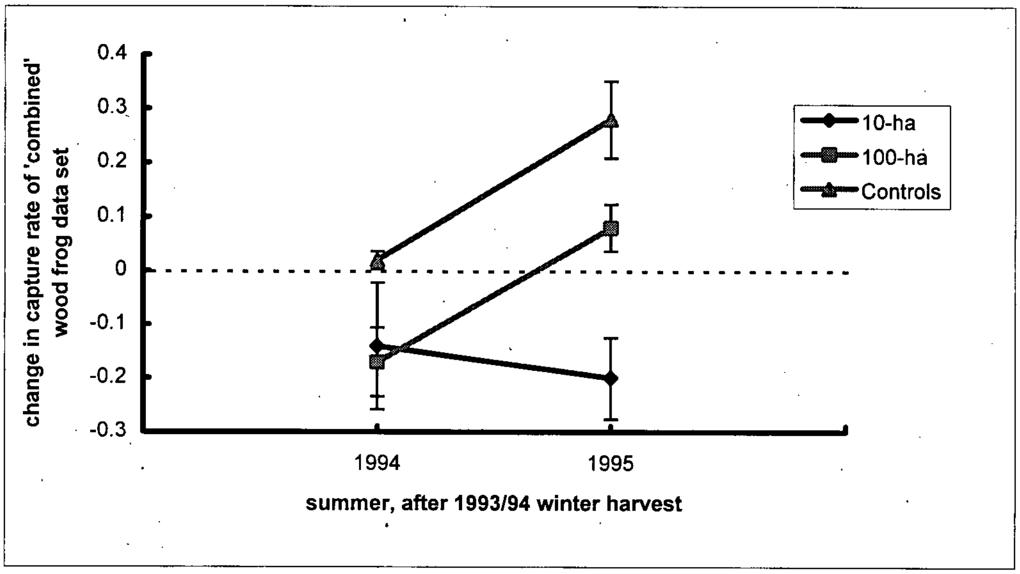


Figure 3.2. Change in capture rate of wood frogs ('combined' data set) among treatments during first and second year after harvesting compared to preharvest capture rate. Bars are standard errors of the means.

Table 3.3. Repeated measures analysis of variance (RM-ANOVA) comparing the change in capture rate of wood frogs ('adult' data set) between the first and second year after harvesting among different treatments.

Between Treatments					
Source	SS	DF	MS	F	P
Treatment	0.13	2	0.06	4.51	0.06
Error	0.10	7	0.01		
Within Treatments					
Source	SS	DF	MS	F	P
Year Effect	0.05	1	0.05	4.33	0.08
Treatment by Year	0.05	2	0.02	2.09	0.19
Error	0.08	7	0.01		

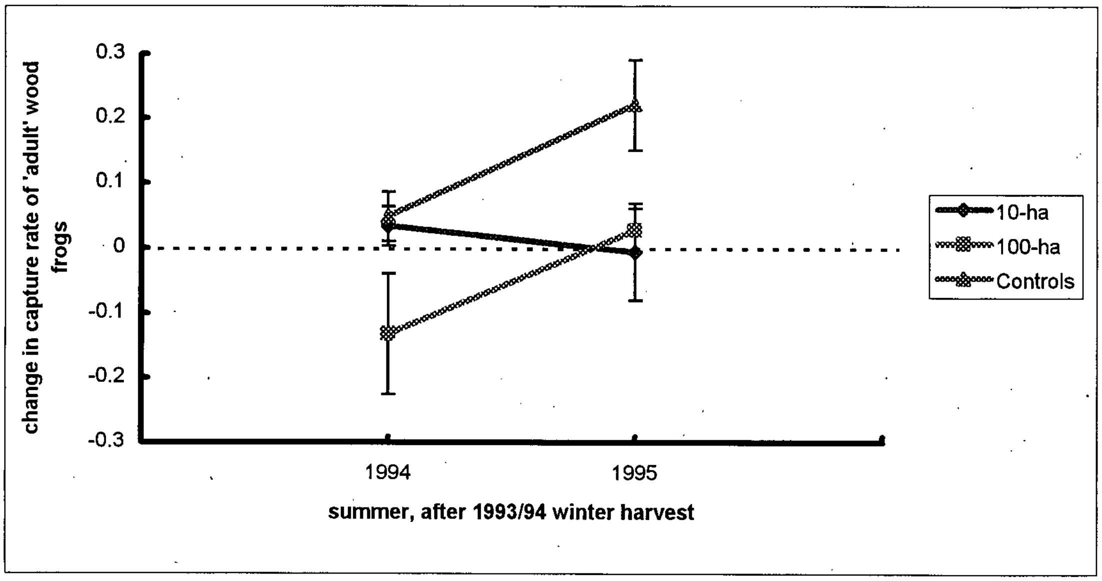


Figure 3.3. Change in capture rate of 'adult' wood frogs among fragmentation treatments first and second year after harvesting, compared to pre-harvest capture rates. Bars are standard errors of the means.

Table 3.4. Repeated measures analysis of variance (RM-ANOVA) comparing the change in mean body length of wood frogs between the first and second year after harvesting among different treatments.

Between Treatments					
Source	SS	DF	MS	F	P
Treatment	386.32	2	193.16	3.08	0.11
Error	439.30	7	62.75		
Within Treatments					
Source	SS	DF	MS	F	P
Year	0.59	1	0.59	0.09	0.77
Treatment x Year	51.03	2	25.52	4.00	0.07
Error	44.66	7	6.38		

control sites (Figure 3.4). Histograms of the lengths of individuals caught within each treatment suggest that proportionately fewer small wood frogs (< 30 mm) were caught in 10-ha sites compared to 100-ha fragments and control sites through time (Figure 3.5).

DISCUSSION

An apparent reduction in wood frog abundance in the 10-ha fragments two years after harvesting was not evident in 100-ha fragments or control sites. The possible negative effects of fragmentation were not evident in the first year after harvesting, and in some cases, the number of 'adult' wood frogs caught apparently increased between 1993 and 1994 (e.g., Site T-1). The effects of fragmentation may not be detectable in the first year, or perhaps for several years, following isolation, and population numbers may actually increase in fragments temporarily (Lovejoy *et. al.*, 1986; Hagan *et. al.*, 1996). Individuals may attempt to follow normal migration routes, and/or disperse into forested areas to escape conditions within clearcuts. If data had been collected only in the first year after harvesting, I would have reached different conclusions regarding the possible effects of fragmentation on wood frogs.

Variability among the three 10-ha fragments in terms of capture rates over the three years may relate to a possible interaction between treatment and habitat. Although two of the 10-ha fragments had their lowest capture rates in 1995, site T-2 had a slightly higher abundance in 1995 than 1994, and the 'adult' data set for this site followed the same general trend as the controls. Site T-2 may have responded differently for two reasons: firstly, it was not completely isolated, a strip of shrubby vegetation associated with a wet area was left along its east side that

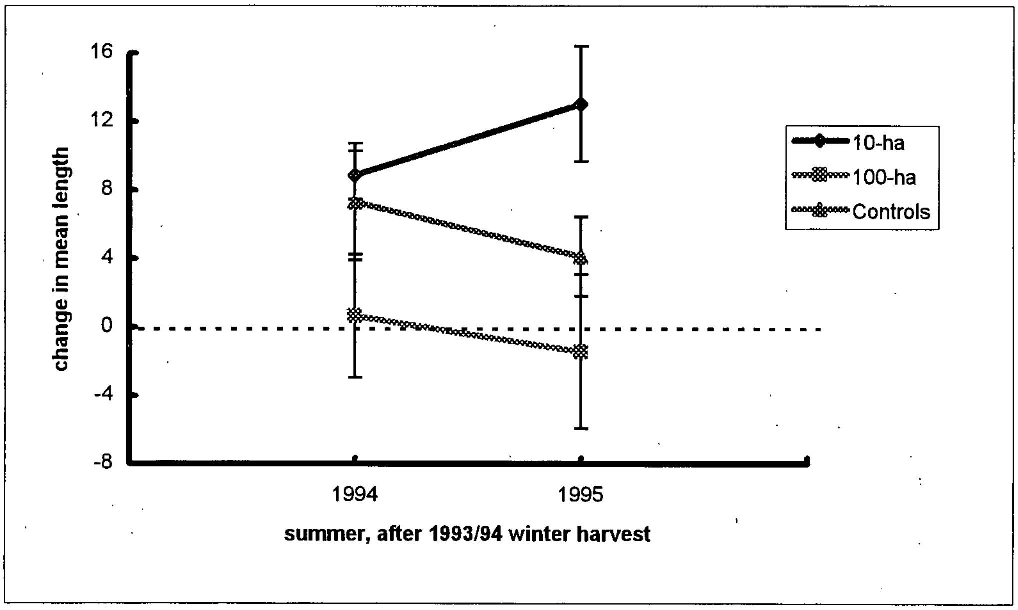


Figure 3.4. Change in mean body length of wood frogs (all sizes combined) among fragmentation treatments first and second year after harvesting compared to preharvest mean length. Bars are standard errors of the means.

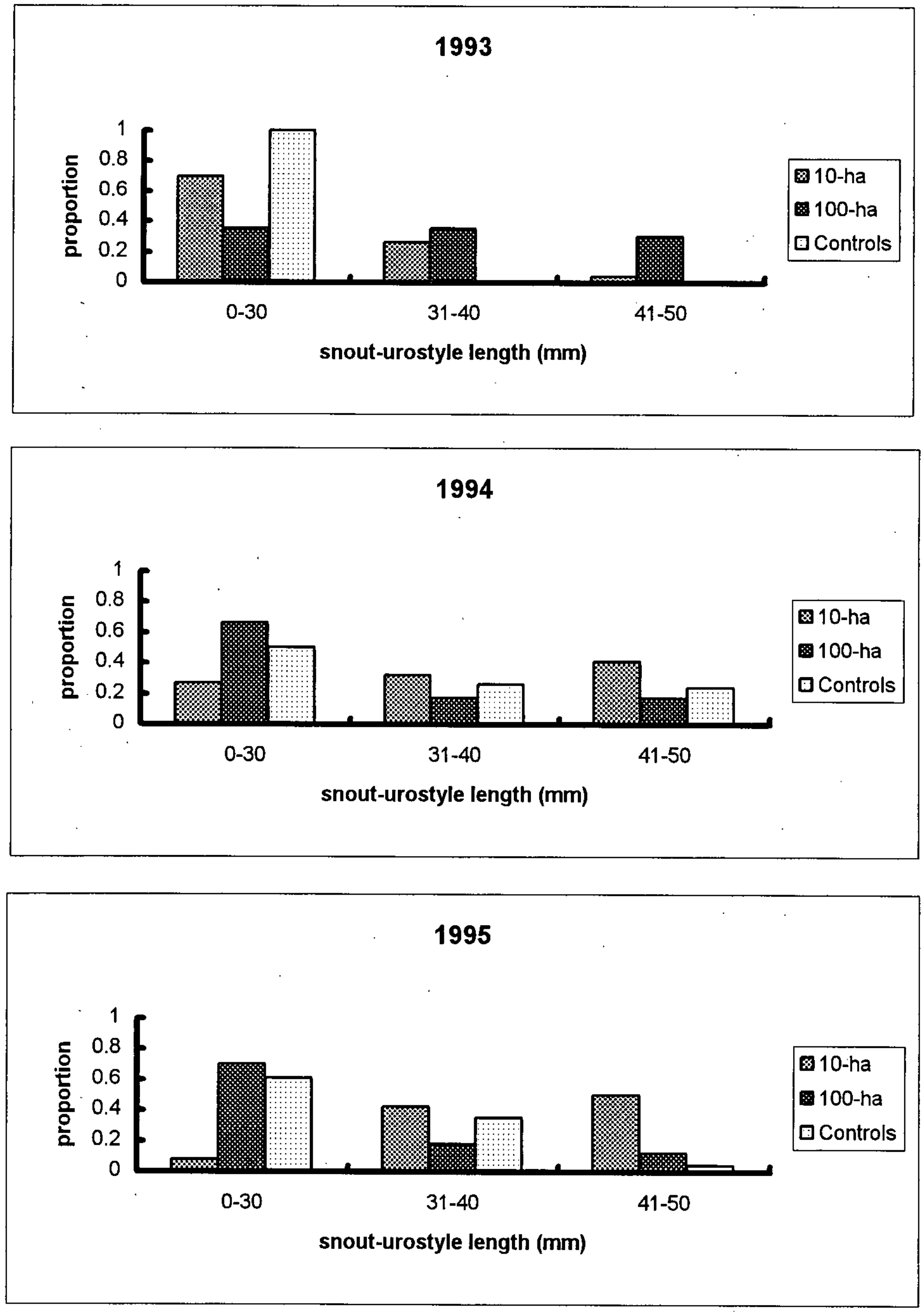


Figure 3.5. Proportion of frogs caught within different length classes among treatments between 1993 and 1995.

connected it to a 40-ha fragment; secondly, the site was highest in terms of percent wetness. In contrast, sites T-1 and T-3 were the driest of the 10 sampling sites, and the decrease in capture rates each year for site T-3 may be due to the fact that this site was the farthest from any standing water (the closest wet area was at least 600-m from the sampling grid). The relationship between fragment size and wetness of the site may exaggerate, or intensify, effects of fragmentation for amphibians. In other words, the smaller and drier the area the greater the probability of retaining fewer amphibians within its boundaries because essential habitat features have been excluded (i.e., breeding sites, moist microsites, etc.). Zimmerman and Bierregaard (1986) came to similar conclusions for frogs in forest fragments in the Amazon, where habitat quality (i.e., density and distribution of wet patches) influenced species richness more than did area relations alone. Related to this is the possibility that drier sites may naturally experience greater annual population fluctuation than wet sites, due to climatic variability within different years. For example, juveniles may only disperse into dry sites when climatic conditions allow for greater success of long distance dispersal (i.e., when there is greater precipitation in late summer than normal).

The increase in average size of wood frogs caught in the three 10-ha fragments two years after harvesting may be due to numerous factors. It may indicate that adults did not breed in or near these sites, that there was increased predation on larvae and/or juveniles, and/or that climatic effects were intensified for smaller individuals, possibly decreasing recruitment into these areas from adjacent sites. The increased average size of wood frogs in the 10-ha fragments may be due to the harsh environment that clear cuts present for some amphibians, particularly newly metamorphosed individuals and developing larvae. Amphibians in Alberta are pond breeding, migrating to their breeding sites mostly from terrestrial hibernation sites (Russell and

Bauer, 1993), and wood frogs have high site fidelity for both the natal breeding site and for overwintering areas (Bellis, 1965; Berven, 1995). Clearcuts are drier, windier and hotter than nearby forested areas in summer (Childs and Flint, 1987), and the nature of an amphibians' skin makes them vulnerable to this climatic variability. These conditions may also increase the risk of predation and affect the amphibian's reproductive phase. The survivorship of larvae may be diminished by an increase in UV exposure at breeding sites within clearcuts or along fragment edges (Blaustein *et. al.*, 1994a), and/or premature drying of wet areas in clearcuts may lead to desiccation of eggs and tadpoles (Pechman *et. al.*, 1989; Zug, 1993). Bellis (1962) suggested that larger individuals can travel farther from water with less risk of desiccation. Larger individuals may be able to travel through clearcuts and avoid desiccation, or they may be the only individuals in the population who will venture into these areas. The recapture of individuals between years in the 10-ha sites, as well as other sites, may indicate that some wood frogs in the Calling Lake area either have relatively small, annual home ranges, or that they are highly philopatric and may have migrated through clearcuts to and from my trapping grids to access breeding sites, summer ranges, or overwintering areas.

Higher temperatures and/or winds associated with clearcuts and forest boundaries (i.e., edge effect), might also decrease the suitability of habitat within and around smaller fragments relative to the most interior section. My results indicate that 10-ha fragments may negatively affect the population of wood frogs more than the 100-ha fragments or controls. This relationship to size of undisturbed habitat may relate to home range size of wood frogs, climatic conditions, and/or movement patterns. Bellis (1965) found that the summer home range size of wood frogs is quite variable in Minnesota (2.93 - 368.73 m^2), but he estimated the mean to be around 64.6 m^2. He predicted that these values were probably conservative due to low recapture rates, and suggested that annual home range size was probably much larger when an individual's breeding site and overwintering area were included. A 10-ha fragment may not provide all aspects of habitat required for maintaining a stable wood frog population year round, forcing amphibians to migrate through clearcuts to find suitable habitat. Lovejoy *et. al.* (1986) found that in the tropical forests of Brazil, a forest patch of 10-ha or less would contain edge-related climatic conditions throughout, and in some areas, clearcuts and second-growth forests contain fewer individuals of some amphibian species than do old-growth forests (Petranka *et. al.*, 1994; Dupuis *et. al.*, 1995). This may indicate that climatic conditions in small fragments are less suitable for sustaining amphibian populations. However, Gascon (1993) found no significant difference in abundance between cohorts of *Epipedobates femoralis* in artificial pools from inside and outside forest environments (i.e., along edges) in Brazil, and Ward and Chapman (1995) found similar abundances of various amphibian species within forests and clearcuts in north-central British Columbia. Zimmerman and Bierregaard (1986) in their study of forest fragmentation and frogs in the Amazon found that the type and number of wet areas retained within a forest stand had a greater influence on amphibian species richness than did the size of the forest fragment itself. My results also indicate that the presence or absence of wet areas within small forest fragments may influence the abundance of amphibians. These seemingly conflicting results may indicate high variability in potential response to forest practices and fragmentation depending upon the species, geographic location, and climatic conditions at the time of the study, as well as the importance of considering specific habitat requirements and patchy distributions of individuals in response to the location of these habitat features. For example, Ward and Chapman (1995) report that there was unusually high precipitation levels during the time of their research, which may have resulted in a more favourable environment for amphibians than would be expected under typical climatic conditions, and the mere presence of water provided by the installation of artificial pools in Gascon's work may have made the environment more suitable for some amphibian species than would normally be found along a forest edge. The presence of individuals within an area does not necessarily reflect the ability of that habitat to sustain a stable, breeding population.

Further research is needed to examine the effects of habitat fragmentation on wood frogs in boreal mixedwood forests. This research should include all amphibian species. However, it is essential that we move away from simply continuing to describe trends related to habitat disturbance, and attempt to determine what the biological impacts of these changes are on ecosystem processes (Saunders *et. al.*, 1991; Didham *et. al.*, 1996). This would allow managers to determine the duration and extent of these trends and find solutions to potential problems.

CHAPTER IV

CONCLUSIONS AND RECOMMENDATIONS

I found a reduction in abundance, and increased average body length, of wood frogs in 10-ha fragments two years post-harvest compared to 100-ha fragments and control sites. Reduced numbers of frogs within smaller fragments reflects trends seen in other taxonomic groups studied elsewhere (e.g., Didham *et. al.*, 1996). Fragmentation may be affecting the wood frog population, as suggested by the increased average size of individuals in the 10-ha sites, by decreasing numbers of breeding adults, thereby lowering reproductive output, by increased predation pressure on juveniles and larvae, and/or by climatic conditions having a greater impact on smaller individuals than larger ones. Bellis (1962) suggested that large frogs are less susceptible to desiccation than smaller ones, and likely disperse greater distances. In the Calling Lake area, small wood frogs may have become restricted in their movements once the area became fragmented. The biological consequences of this reduction in number of small frogs for the overall wood frog population, as well as for the ecosystem, will depend upon the duration and extent of fragmentation (i.e., degree of isolation, size of clearcuts, location of clearcuts relative to breeding sites and movement corridors, and period during which clearcuts are inhospitable to small frogs).

Variability in the abundance of wood frogs within the 10-ha fragments over the three year period may be related to differences in habitat attributes among sites. Sampling site T-2 (10-ha) was one of the wettest sites in the study area and was not completely isolated. This may have ameliorated fragmentation effects for wood frogs in that site. Zimmerman and Bierregaard (1987) suggest that habitat characteristics (i.e., the number, location, and type of wet patches) within a site may override species-area relations for amphibians in tropical forest fragments. For example, a large tract of forest which does not contain essential habitat features (e.g., breeding sites) may be less suitable than a smaller fragment with numerous wet patches. Related to this is the importance of distinguishing between 'source' and 'sink' areas (Pulliam, 1988). Areas which are important reproductive centres support the surrounding sink population. Source areas may have a lower abundance of a particular species than do sink areas, which can result in misleading information when determining effects of habitat disturbance, as well as investigating prime habitat for species, based on abundance estimates alone. For example, site H-1 (100-ha) contained the highest capture rates of wood frogs in all three years at Calling Lake, but it was also one of the driest sites. This site may serve as a sink area, and/or it may be important summer or winter habitat. Both source and sink areas, as well as the relative use of various habitat types by different species throughout the year, should be delineated.

Although my study indicates that a negative effect of fragmentation may exist for wood frogs in the boreal mixedwood forests of Alberta, constraints of my sampling design limit my interpretation. For example, low capture and recapture rates in the area, inherent annual variability in wood frog populations, and habitat heterogeneity among sampling sites, likely reduced my ability to detect treatment effects by increasing the variance within treatments. As well, the mechanism which acted upon wood frog abundance within the 10-ha fragments is unclear. For example, it may have been the size of the fragment, edge effects, or the need to move through clearcuts which may have reduced population numbers within the 10-ha fragments. To advance our management for biodiversity it is essential that we do more than simply describe disturbance patterns when we try to determine biological impacts on ecosystem function in fragmented forests (Saunders *et. al.*, 1991; Didham *et. al.*, 1996).

A sampling design that included ways of increasing the power to detect a treatment effect, and strategies to eliminate competing hypotheses, would have greatly improved my study. For example: 1) the use of drift fencing and/or more traps would have increased capture rates; 2) additional replicates would have reduced some of the variability within treatments as a result of specific habitat features in some sites; 3) the wetness of each site should have been standardized (however, this is very difficult to do because many small wet patches are not on maps or air photos, and they are highly variable); 4) individuals could have been radio tagged to follow movements to and from breeding sites to determine if clearcuts impede their movements; and 5) wood frogs could have been trapped within clearcuts and along edges before and after harvesting to determine if numbers were subsequently reduced in those areas after harvest.

When assessing potential impacts of timber extraction and fragmentation on amphibian populations management guidelines must take into account specific habitat requirements and the patchy distribution of these habitat features. An essential feature of sound ecosystem management is understanding the habitat requirements of all wildlife species at the stand, as well as, landscape levels. Little is known of the habitat requirements of amphibians in the boreal mixedwood forest, especially in the terrestrial environment. My study indicates that at the stand level wood frogs may be associated with relatively large coarse woody material (CWM3) within boreal mixedwood forests. Other studies have found amphibians, especially salamanders, associate with CWM for protective cover from predators and climatic extremes (Jaeger, 1980; Aubry *et. al.*, 1988; Aubry and Hall, 1991). Amphibians may depend more upon habitat features which provide cover and moisture, such as CWM, rocks, and moss when an area becomes disturbed (e.g., clearcut). The boreal forest is a mosaic of habitat types, one of which is the mixedwood ecoregion (Bonan and Schugart, 1989). At this time it is unknown what the relative importance of the various ecoregions are for amphibians in the boreal forest, or whether all habitat types or wet patches are used by amphibians. For example, elsewhere amphibians have shown variable associations with conifer stands (Heatwole, 1961; Bennett *et. al.*, 1980). In the face of broad-scale, landscape level changes taking place within this ecosystem we cannot begin to adequately manage for amphibians until we know more about their specific habitat requirements.

Maintaining relatively large forested areas, with a variety of habitat types and wet patches contained within their boundaries, may ensure that a significant proportion of resident wood frog populations are sustained. Research into the effects of fragmentation on wood frog populations should continue to determine the duration, as well as the extent, of these effects and the mechanisms at work. This fragmentation research should be expanded to include all amphibians species. Research should investigate movement patterns and the survival rate of cohorts in a fragmented landscape, as well as the role various types and sizes of wet patches play in maintaining amphibian populations in the boreal mixedwood forest. Furthermore, community level studies should be initiated to determine the habitat requirements of all amphibians within the boreal ecosystem.

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APPENDIX 1

Habitat Variables Used in Forward Stepwise Multiple Regression

Variable Grouping and Measurement	Variable	Code
Shrubs (Number of individual plants >50 cm high)	*Alnus crispa* (alder)	ALCRISPA
	Lonicera involucrata (bracted honeysuckle)	LONIC
	Ribes lacustre (black gooseberry)	RIBESLAC
	Rosa sp. (various rose species)	ROSA
	Rubus idaeus (wild red raspberry)	RUBUSID
	Symphoricarpos occidentalis (snowberry)	SNOW
	Viburnum edule (lowbush cranberry)	VIBURNED
	Shrub species richness (Number of different shrub species within the plot)	SHRUBRICH
Saplings and poles (< 8 cm dbh) (Total number of stems per plot, per species)	*Alnus crispa*	SAPOLE1
	Populus tremuloides (trembling aspen)	SAPOLE2
	Salix sp. (willow)	SAPOLE3
	Populus balsamifera (balsam poplar)	SAPOLE4
	Betula papyrifera (white birch)	SAPOLE5
	Picea glauca (white spruce)	SAPOLE6
	All species of saplings and poles combined (Number of stems of all species)	TOTSAPOL
Trees in four size classes, plus all size classes combined (Total number of stems per plot, per species)	*Populus tremuloides*	TREM1, TREM2, TREM3, TREM4, SP2
	Salix sp.	SALIX1, SP3
	Populus balsamifera	BAL1, BAL2, BAL3, SP4
	Betula papyrifera	BET1, BET2, SP5
	Picea glauca	PIC3, PIC4, SP6
	Tree species richness (Number of tree species of all size classes combined; and of each size class individually)	TREERICH SIZE1; SIZE2; SIZE3; SIZE4
Coarse woody material in four size classes (0<2; 2<5; 5<11; 11+ cm diam.), and a total of all size classes combined	Coarse woody material	CLASS1 - 4, CWMSUMM
Canopy closure (%)	Canopy closure	CANOPY
Leaf litter depth (cm)	Leaf litter depth	LDEPTH
Percent ground cover	All non-woody green vegetation < 50 cm tall	ALLGREEN
	Grasses and sedges	GRASS/SEDGE
	Forbs	FORBS
	Coarse woody material	WOODY
	Mosses and ferns	MOSS/FERN
	Leaf litter	LEAFLITT
	Shrubs	SHRUBS
		Total number of variables = 51