HABITAT USE BY LONG-TOED SALAMANDERS (*Ambystoma macrodactylum*) AT THREE DIFFERENT SCALES

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ABSTRACT

HABITAT USE BY LONG-TOED SALAMANDERS AT THREE DIFFERENT SCALES

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During the summers of 1994 and 1995, habitat use of long-toed salamanders (*Ambystoma macrodactylum*) at a microhabitat, macrohabitat and landscape scale were examined to determine the habitat associations for this species around Hinton, Alberta Canada. Relative abundance was used as an index of habitat use and was estimated by using pitfall arrays and egg counts.

The microhabitat scale indicated salamanders were clustered close to the breeding ponds, on sloped terrain with thick litter. A comparison of relative abundance in different habitat types (forests, clearcuts and wet areas) resulted in comparisons with low power and prevented drawing definite conclusions. The landscape scale, where breeding population size was compared with the amount of harvesting around breeding ponds, indicated no relationship between breeding population size and total harvested area. Long-toed salamanders appear to be habitat generalists at a landscape scale but may select certain habitat features when establishing home ranges.

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GENERAL INTRODUCTION

The long-toed salamander (*Ambystoma macrodactylum*) is a mole salamander found throughout western North America (Ferguson 1961, Stebbins 1985, Russell and Bauer 1993). In Alberta, the long-toed salamander is considered rare and is "Red-listed" by Alberta Forestry, Lands and Wildlife. Red-listed species are considered to be "in serious trouble" (Anon. 1991). *Ambystoma macrodactylum* is thought to be vulnerable to habitat alteration associated with industrial, recreational or transportational development (Anon. 1991), yet no study has specifically examined the distribution of this species and its associated habitats. In this study, I examine habitat use of long-toed salamanders in west-central Alberta at a microhabitat scale (habitat features), macrohabitat scale (habitat types), and at a landscape scale to determine the habitat associations for this species and provide a better understanding of their selection process.

Amphibians are often one of the most abundant vertebrates in an ecosystem (Burton and Likens 1975, Jaeger 1980, Southerland 1986), yet are often overlooked in wildlife studies. In 1989, amphibians began receiving more attention when declines in their populations were noted in many regions of the world (Wake 1994). It became apparent that information concerning the distribution and abundance of many amphibian species was lacking. These data are essential if future declines in amphibian populations are to be detected. In addition, little was known about the specific habitats which supported amphibian populations. The habitats used by amphibians need to be further investigated because habitat alteration may have caused some amphibians to decline in numbers (Johnson 1991, Wake 1994, deMaynadier and Hunter 1995).

Because amphibians often comprise a large proportion of the biomass in an area, they are believed to be an important component in the food web and in nutrient cycling (deMaynadier and Hunter 1995). Amphibians feed on invertebrates that are not normally eaten by other larger vertebrates, thereby, serving as an important intermediate in food webs (Pough 1983). Amphibians may regulate populations of soil invertebrates that mechanically break down organic material and affect the rate of decomposition and cycling of nutrients in an ecosystem (Burton and Likens 1975).

Amphibians may be more susceptible to habitat alteration are than most other vertebrates. Their permeable skin causes them to be very susceptible to desiccation. Many species require both aquatic and terrestrial habitats to complete their life cycle, and amphibians do not migrate long distances, so small-scale habitat disturbances may have large consequences on local populations. It is important to understand the relationship between amphibian populations and their habitats so we can better manage for their continued existence.

The distribution and population size of amphibians can vary considerably in space (Heatwole 1961), which suggests that the ecological requirements for some amphibian species may confine them to specific habitats (Bury et al. 1980). Studies of habitat use by urodeles have focused on plethodontid salamanders, which breed in damp terrestrial areas and are not restricted to areas near ponds (Pough et al. 1987, Corn and Bury 1991, Diller and Wallace 1994). Few studies have examined habitat use by salamanders of the genus *Ambystoma*, the mole salamanders, because they are more difficult to census and survey (Welsh 1990, Bury et al. 1991, Aubry and Hall 1991).

Mole salamanders are only conspicuous during the breeding season when adults migrate from their overwintering sites to breeding ponds in the early spring. Once breeding and egg laying are finished, adults leave the ponds and move underground, often into small mammal burrows (Douglas 1981, Semlitsch 1981). With the exception of moving to the surface to feed on invertebrates on humid nights, adults remain underground for the rest of the year making it difficult to collect information on their terrestrial, post-breeding distribution.

The distribution of organisms is often determined by habitat because habitat influences reproductive success, predation, competition and the availability of food and shelter (Andrewartha and Birch 1967, Morrison et al. 1992). By examining the distribution and abundance of individuals in relation to their environment, some habitat associations may be revealed (Dueser and Shugart 1978, Holomuzki 1986, Bergin 1992, Smith and

Connors 1993). This does not necessarily mean that habitat is the only factor affecting the distribution and abundance of individuals. More often, it is interactions between the habitat, conspecifics, predators, and prey that control distribution. Uncovering habitat associations is a first step in understanding what influences a species' distribution.

Because habitat in a region is a heterogeneous mosaic of patches varying along a continuous gradient of scales (Kotliar and Wiens 1990) habitat selection should also be viewed as a hierarchical process occurring at various scales (Wiens 1989, Kotliar and Wiens 1990, Orians and Wittenberger 1991, Morris 1992). The size of patches and how an organism perceives different patches influence habitat use. If abundance is associated with a large patch size that is described as a specific habitat type, then we can infer that the individuals prefer certain habitat types over others. If individuals of a species are associated with several habitat types, this suggests that the species is opportunistic in habitat use at that scale. However within these large patches individuals may use some areas more than others which suggests that habitat selection is occurring on a smaller scale within a habitat type (Morris 1984). By examining habitat use at different scales, inferences can be made about why individuals choose some areas over others. Previous studies have investigated habitat use at different scales for birds (Orians and Wittenberger 1991, Bergin 1992), small mammals (Morris 1986, Morris 1992) and plants (Collins and Glenn 1991).

No study has specifically examined multiple scales of habitat use for ambystomatid salamanders.

This study examines the terrestrial habitat use of long-toed salamanders in west central Alberta at three different scales in an effort to determine associated habitats. Chapter one addresses the question of whether individuals within populations exhibit a distribution that is suggestive of differential habitat use. Features of the habitat (microhabitat) are examined to test whether habitat features explain some of the variation in relative abundance of salamanders around breeding ponds. In Chapter two, I examine habitat use at a macrohabitat scale and at a landscape scale. For both scales, the focus is on the impact that logging may have on the habitats used by long-toed salamanders. I examine whether the relative abundance of individuals differs in different habitat types (i.e. forested, clearcut and wet areas) and at the landscape scale I examine whether breeding population sizes vary with various amounts of harvested areas in the landscape.

CHAPTER 1

DISTRIBUTION AND HABITAT USE OF LONG-TOED SALAMANDERS AT A MICROHABITAT SCALE

INTRODUCTION

Individuals may be distributed in three ways. A random distribution indicates that any locality has an equal probability of being used as any other locality. In terms of habitat selection, a random distribution suggests that either no selection is taking place or, selection is taking place, but the selected resources are distributed at random. An even distribution often indicates that the species in question is territorial. Long-toed salamanders are not likely evenly distributed because salamanders of the genus *Ambystoma* are not considered to be territorial (Martin et al. 1986). Finally, a clustered distribution suggests differential habitat use may be occurring (Patton 1992).

A clustered distribution is a result of interactions among many processes (Andrewartha and Birch 1967) that cause either differential survival, with individuals dying in the poor sites, or individuals actively selecting certain sites over others, presumably sites that provide good chances of survival and/or reproduction. Examining the distribution of individuals in association with specific habitat features can often reveal the features used as cues during the selection process or features that are associated with those being used as cues (Dueser and Shugart 1978, Holomuzki 1986, Bergin 1992, Smith and Connors 1993).

Specific habitat features have been associated with other species of salamanders. Deep litter (Pough et al. 1987, Corn and Bury 1991), old trees (Welsh 1990, Petranka et al. 1994), and large amounts of downed wood (Bury et al. 1991) were all correlated with a greater abundance of plethodontid species. No study has explicitly examined the habitat features associated with the terrestrial abundance of long-toed salamanders.

In this chapter, my first objective was to determine whether the distribution of long-toed salamanders around individual ponds suggested that differential habitat use was occurring (i.e. were individuals clustered in some areas around a pond more than other areas). My next objective was to examine microhabitat use to determine whether site specific habitat features explained the observed distribution of individuals. I use relative abundance of individuals at sites as a measurement of habitat use. Habitat features included both biotic and abiotic features in the study area as suggested by Karr (1981).

METHODS AND MATERIALS

Study sites were near Hinton, Alberta, Canada on the eastern slopes of the Rocky Mountains and adjacent to Jasper National Park within the Foothills Model Forest (Fig. 1.1).

Relative Abundance

In 1994, four breeding ponds were selected as study sites (Fig. 1.2). I selected these ponds based on the abundance of long-toed salamander eggs (> 9000 eggs, see Table 2.1), road access, and the variety of habitats surrounding each pond which provided a good representation of habitats in the region.

Pond 1 (Fig. 1.3) was surrounded by a continuous forest. White and black spruce (*Picea glauca, P. mariana*) grew adjacent to the pond. Further from the pond, the common tree species were white spruce, lodgepole pine (*Pinus contorta*) and trembling aspen (*Populus tremuloides*). Pond 2 (Fig. 1.3) was surrounded by lodgepole pine and black spruce forest. Recent clearcuts (within five years) and regenerating clearcuts (12-15 years old) with trembling aspen and lodgepole pine saplings were located within 200 m of the pond. Pond 3 (Fig. 1.3) was surrounded by a white spruce forest with wet areas populated with sedges (*Carex* sp.) and bog birch (*Betula glandulosa*). Pond 4 (Fig. 1.3) was surrounded by poorly regenerating 25-35 year old clearcuts with scattered small balsam popular (*Populus balsamifera*) and white spruce saplings. The dominant vegetation was shrub species consisting of rose (*Rosa* sp.), buffaloberry (*Shepherdia canadensis*) and willow (*Salix* sp.). Wet areas of bog birch and sedges were also present.

Pit-fall arrays (Crump and Scott 1994) were used to sample salamanders. Pit-falls are considered the most effective method of continuously sampling terrestrial amphibians because they overcome the biases and habitat destruction associated with time-constrained searches (Crump and Scott 1994). During the spring of 1994, aerial photographs were used to locate six random positions for pit-fall arrays within 500 m of the four ponds (Fig. 1.3). A stratified random design was used to sample a more even representation of the area around the pond. Three arrays were randomly located within 250 m of the pond and another three arrays were randomly located between 250 m and 500 m from the pond. A maximum of 500 m was chosen because previous studies on ambystomatid salamanders found that movement rarely exceeded 500 m from the breeding pond (Whitford and Vinegar 1966, Douglas 1981, Semlitsch 1981). The location of each site was marked with flagging tape and a pitfall array was installed.

An array (Fig. 1.4) consisted of three fences made from 5-m lengths of 40 cm opaque heavy duty plastic sheeting radiating from a central point. No effort was made to orient each arm in any specific direction. At the ends, and on either side of the fences, a 3-L tin can was dug into the ground with the top opening flush with the ground. The fence was also dug at least 5 cm into the ground and supported by stapling the plastic onto 60 x 5 x 2 cm pieces of wooden lath, that were driven into the ground. Square pieces of plywood large enough to cover the opening of the can, was suspended over each can using sticks as props, to prevent desiccation and flooding. A handful of moss and leaf litter, approximately 50 to 100 mL of water, and a small twig that was placed upright in each can to allow small mammals to escape were in each can.

Twenty-four arrays were erected and used from July to August 1994 and from June to August 1995. During the summer of 1994, one array around Pond 2 and one array around Pond 4 were regularly destroyed by bears (*Ursus americanus*). Data from these arrays were not used in subsequent analyses for that year. Pit-fall arrays were checked every 4-5 days. Snout-vent length (SVL) of captured salamanders was measured to the nearest millimetre using a 15-cm plastic ruler. Mass was determined using a 10-g AVINET PRECISION®spring scale and measured to the nearest tenth of a gram. To ensure salamanders were not counted twice, individuals were marked with a unique toe-clip code. More salamanders were caught than was anticipated and few individual codes were still available by the end of 1994. For this reason, salamanders in 1995 were given a toe-clip code that was unique only to the array of capture. Because an individual's sex could be accurately determined only during the breeding season, it was not recorded. Salamanders were then released 10 m from the array on the opposite side of the fence from which they were captured.

To sample as wide a range of the habitat characteristics as possible another 10 pitfall arrays were installed in the spring of 1995 (Fig. 1.3) as follows: two arrays were placed in the centre of wet areas (at least 30 m from the forest edge) that were within 500 m of Pond 3; two arrays were placed around Pond 2, in the centre of three-year old clearcuts (at least 50 m from the forest edge) which were within 500 m of the pond; and the remaining six arrays were placed around Ponds 1, 2, 3 and 4 in habitats which had little to no representation from the 24 randomly placed arrays.

Habitat Characteristics

Habitat characteristics were chosen using the following criteria: (1) they were suspected to influence the distribution of salamander populations (Johnson 1981); (2) they could be quickly and precisely measured (Dueser and Shugart 1978); and (3) they would be few in number with little correlation between one another (Johnson 1981).

Four nested sampling units were used (Noon 1981) : (1) a 0.04-ha circular plot; (2) a 0.008-ha circular plot; (3) four 12.5 m transects; and (4) 1 m^2 quadrat (Fig. 1.5). Total trees by species and diameter at breast height (DBH) classes (26 cm > DBH ≥ 26 cm) were tallied within the 0.04-ha plot. Total saplings (trees < 8 cm) were tallied within the 0.008-ha plot. Length and width of downed wood ≥ 7 cm in diameter along the four transects were measured and recorded. A diameter of 7 cm was chosen because this size provided enough cover for an average sized (10 cm) salamander to hide. Percent ground cover of shrubs, herbs and moss was estimated in the 1-m^2 quadrates. Shrubs species included all woody plants except dwarf woody species (eg. twin flower *Linnaea borealis* and bog cranberry *Vaccinium vitis-idaea*). Herbs included all nonwoody plants, grasses, sedges, horsetails and dwarf woody species not included as shrubs. The slope and aspect of the land was measured across the plot in the direction of the greatest gradient using a clinometer and a compass, respectively.

Soil composition was estimated from a soil pit that was dug at a random location within the 0.04-ha plot. Soil composition for the top soil horizon was estimated using the taste, feel, shine and ribbon field tests (Anon 1994). These tests classify soil on the basis of the relative amounts of sand, clay and silt present. Litter depth was measured to the nearest centimetre at one site along each of the four transects. The litter layer was defined as the accumulated organic material overlaying mineral soil and was measured from the top of the forest floor to the top of the first mineral soil horizon. In areas where mineral soil was not present within 60 cm from the surface (i.e. organic soils), the litter layer was measured from the top of the forest floor to the position in the profile where organic matter was not recognizable. Soil pH was measured using an E.W. SYSTEM SOIL TESTER®

pH meter.

Habitat characteristics were quantified at the 34 arrays around the four ponds during a 4-wk period at the end of July and the beginning of August. At most arrays, habitat characteristics were quantified in 1994. Arrays installed in 1995 had the habitat measured between the end of July and the beginning of August in 1995. It was not possible to measure habitat again in 1995 at the arrays measured in 1994 because of time constraints. I assumed there was little interyear variation.

Statistical Analysis

Capture data were standardized for trap effort. Some pitfalls flooded on rainy nights which potentially allowed salamanders to escape and reduce captures at wet sites relative to drier sites. Also, incidental disturbances by animals reduced the number of nights that some arrays functioned properly. Therefore, the total number of salamanders caught at each array was standardized to total captures per 100 trap nights (Corn and Bury 1991). In addition, emerging juveniles were not included in the analyses. Emerging juveniles may use habitats differently from adults (McKenzie and Storm 1970). All juveniles caught emerging from the pond were less than 40 mm SVL. Therefore, only salamanders with a SVL greater than 40 mm were included in all analyses.

A t-test was used to determine whether mean captures for the randomly placed arrays were significantly different between years for each pond. Analysis of covariance (ANCOVA) was used to determine whether salamanders were clustered in some areas more than others. Only captures at the random arrays were used and captures for the two years at an array were treated as replicates. A clustered distribution was assumed if there was a significant difference in captures among the arrays for a pond. Any impact that distance from pond had on captures was accounted for by including the distances from the pond to the arrays as a covariate. In addition, differences in relative abundance among the four populations caused by differences in population sizes were accounted for by including a variable that distinguished the pond where each individual was captured (Snedecor and Cochran 1989). Captures around a study pond were assumed to come from a single population (i.e. they all used the study pond for breeding).

Stepwise multiple regression was used to determine whether any habitat features explained variation in salamander abundance over the two years. Captures from all the arrays around the four ponds for both years were used. The habitat variables used in the regression analysis are shown in Table 1.1. I included dummy variables for pond population and for year.

The residuals were examined to determine whether the data conformed to the assumptions of homoscedasticity, normality, and linearity

(Gutzwiller and Anderson 1986, Snedecor and Cochran 1989). Transformation of the standardized adult captures/100 trap nights was necessary and the square root transformation produced data which satisfied the assumptions for both multiple regression and ANCOVA. All analyses were performed using SPSS PC^+, version 4. All tests used an significance level of 0.05.

RESULTS

Captures

A total of 1071 salamanders were captured during 1994 and 1995 (including juveniles). A total of 36 salamanders were recaptured and only six of these were caught at a different array from initial capture (Table 1.2). One individual was caught at the end of July 1994 and was recaptured on the other side of the pond during the spring of 1995. Only one array did not catch any salamanders over the two summers. This was located at array 1, around Pond 4, in a poorly drained area dominated by bog birch and sedges.

Distribution and Habitat Associations

The mean number of salamanders caught around each pond was not significantly different between years for any of the ponds (t-test; Pond 1, df = 10, $t = 0.07$, $P = 0.94$; Pond 2, df = 9, $t = -0.69$, $P = 0.51$; Pond 3, df = 10, $t = 2.14$, $P = 0.06$; Pond 4, df = 9, $t = 0.55$, $P = 0.59$; Fig. 1.6). Salamander captures among arrays were significantly different (Table 1.3, ANCOVA, $P < 0.01$) which suggests that salamanders were clustered in some areas more than others within 500 m of the breeding ponds. Distance from the pond to the capture site (i.e. the array) was significant ($P < 0.05$) which indicates that more salamanders were captured at arrays closest to the breeding ponds. Mean captures around the four ponds was also significantly different ($P < 0.001$) which indicates that the four populations varied significantly in size.

The variation found for each habitat feature is shown in Table 1.4. Backward multiple regression was significant ($P < 0.0001$) (Table 1.5) with an r^2 value of 0.62. Independent variables with significant ($P < 0.05$) partial regression coefficients were distance from pond, litter depth, and slope (Table 1.6). The dummy variable representing the population around Pond 2 also explained some of the variation in relative abundance, indicating captures around this pond were greater compared with the other three ponds (Table 1.6).

DISCUSSION

Captures

Captures were assumed to reflect relative abundance. This means that salamanders must be moving about on the forest floor some nights and behaving similarly (i.e. moving similar distances) so the pitfalls arrays would capture a representative sample at all sites. It is possible that arrays with few captures had many salamanders in the vicinity, but little movement occurred because an ample supply of food was present or conditions were not suitable for foraging (i.e. surface was too dry) so salamanders remained underground. If the former were the case and individuals did not have to move very far to obtain the necessary resources, recaptures of the same individuals at an array would be expected to be high. However, few recaptures occurred at original capture sites (30 out of 1071 captures), and the six individuals captured at different arrays travelled over 100 m. Sheppard (1977) found long-toed salamanders generally exploited a large area during the summer, with males and females having an average home range size of 167.5 m^2 and 115.6 m^2, respectively. Because I attempted to catch individuals only after migration to and from the breeding pond was completed, I believe that a given array caught individuals whose home range it overlapped and individuals were captured moving from one site within its home range to another, regardless of the availability of food resources.

If above ground conditions were not suitable for salamanders to forage at night (i.e. conditions were too dry) at some arrays, then salamanders would be forced to remain underground until moisture conditions improved. Prey is believed to be less abundant in underground burrows compared with the litter layer of the forest floor (Fraser 1976). If individuals need to come up to the surface to obtain their necessary energy requirements, very dry sites might prevent them from doing this and cause an increase in mortality or a decrease in fitness. It is unknown whether long-toed salamanders will remain in an unsuitable site or move on as soon as appropriate conditions arise. Raymond and Hardy (1991) examined the effects of a clearcut on a population of *Ambystoma talpoideum* and concluded that the clearcut caused some individuals to move to the other side of the pond. It seems likely that long-toed salamanders will also move to new sites if conditions prove to be unfavourable, therefore I assumed that few captures at an array over the course of a summer indicated that the site was not as suitable for salamanders as other arrays which caught numerous individuals.

Habitat Associations

Salamanders were clustered in some sites more than others. This means that salamanders were either actively choosing sites (i.e. habitat selection), or there was differential survival occurring at different sites. I could not differentiate between habitat selection versus differential survival, however, evidence suggests that ambystomatid salamanders will move from unfavourable areas (Raymond and Hardy 1991) and lends support that long-toed salamanders will select areas that are favourable.

Habitat features associated with a greater abundance of salamanders were thick litter and sites on slopes. The importance of litter layer to salamanders has been reported for other species such as red-spotted newts, *Notophthalmus viridescens*, red-backed salamanders *Plethodon cinereus* (Pough et al. 1987), and del norte salamanders, *Plethodon elongatus* (Diller and Wallace 1994). A thick litter layer reduces moisture loss from the ground and may also increase prey abundance for salamanders (Welsh and Lind 1995). In addition, a thick litter layer has been associated with more tunnels and burrows created by small mammals. Semlitsch (1981) found *A. talpoideum* was associated with burrows or tunnels created under the leaf litter by small mammals. *Ambystoma macrodactylum* may also rely on small mammals for creating suitable cover, when natural crevices are not present.

Sites located on a gradient have also been positively associated with the abundance of southern torrent salamanders, *Rhyacotriton variegatus* (Welsh and Lind 1995) and western red-backed salamanders (Corn and Bury 1991). In these studies, it was not slope per se that was directly associated with salamander abundance, but the talus found at the bottom of the slopes. No talus was present near any of my arrays. At my study sites, many of the relatively flat areas were very wet with the soil saturated for much of the summer. Possibly, long-toed salamanders were avoiding these wet sites because they did not provide adequate food and/or cover compared with drier sites.

Salamander abundance decreased with distance from the breeding ponds. I assumed that all adults caught around the four study ponds used the study ponds for breeding. It is very likely that other ponds or ditches proximate to the study ponds were also used for breeding purposes. For example, Pond 4 had other permanent ponds within a kilometre. Some individuals caught at the most distant arrays around Pond 4 may have been from a closer breeding pond (i.e. a different breeding population). This would inflate the relative abundance estimates for those distant arrays. Therefore, the significant association found between salamander abundance and distance from the breeding pond may be even stronger than my result suggests.

Pond 2 had a larger breeding population based on capture data and confirmed with egg count data (see Chapter 2) compared with the other three study ponds. This suggests that something about the pond or the terrestrial habitat surrounding the pond provides better reproductive success and/or adult survival compared with the three other study ponds. The mean litter depth for arrays around Pond 2 was greater than the other three ponds (Table 1.4) and may therefore provide more cover and/or food. In addition, Pond 2 was the largest of the four ponds and may simply support a larger breeding population by providing more egg laying sites, food, and cover for growing larvae.

In my study, soil pH was not a significant predictor of salamander abundance. PH only ranged from 6.3 - 7.0, which may not have exceeded the tolerance of *A. macrodactylum.* Wyman and Hawksley-Lescault (1987) found that soil pH influenced the densities of *Plethodon cinereus.* Their pH values ranged from 2.7 - 5.8 and they found that the acute lethal pH for *Plethodon cinereus* was between 2.5 and 3. Based on their findings, it seems likely that the soil pH in the Hinton area was not a limiting factor for long-toed salamanders.

In my study, the number of trees in the plot, and the type of trees (coniferous versus deciduous) were not significantly associated with salamander abundance nor was the number of trees with a DBH $\geq$ 26 cm (suggesting mature forest). In contrast, other species of Ambystomatid salamanders have been associated with mature forests. *Ambystoma gracile* was found to be associated with old growth forest in the American northwest (Bury et al. 1991, Corn and Bury 1991, Aubry and Hall 1991) and Semlitsch (1981) found *A. talpoideum* to be associated with mature forest in South Carolina, although no preference for forest type (pine plantation versus hardwoods) was detected. In my study, most of the arrays around Pond 4 that caught salamanders were located in shrubby clearcuts that had not re-established a tree canopy. Perhaps these poorly regenerating clearcut areas in my study still provided habitat attributes suitable for long-toed salamanders. Pond 4 had a dense shrub cover (Table 1.4) . Shrub cover was not a significant variable in the multiple regression analysis, however the combination of many rotting roots and dense shrub cover could offer enough protection from desiccation and provide crevices for salamanders to move underground and could compensate for the lack of tree canopy cover in this area.

Most studies that have examined habitat use of amphibians have focused on species of the family Plethodontidae. Typically, downed woody debris was associated with salamander abundance (Corn and Bury 1991) because *Plethodontid* species require moist rotting logs for egg laying. In contrast, Ambystomatid species do not use downed woody debris for egg laying. Semlitsch (1981) found that the areas with the highest activities of *A. talpoideum* were not associated with downed woody debris, and is consistent with my results for *A. macrodactylum.*

Habitat use can be affected by predation and inter- and intraspecific competition (Jaeger 1971, Van Horne 1983, Patton 1992). Because adult long-toed salamanders exude a toxic substance when threatened, they have few mammalian predators. Snakes are a common predator of adult salamanders (Burton and Likens 1975) but in the Hinton area, snakes are very rare (Bonar pers. comm., Graham pers. obs.). The long-toed salamander is the only salamander found in the area, so competition with other salamander species would not affect habitat use. In addition, mole salamanders are generally considered to be nonterritorial (Alvarado 1967, Martin et al. 1986) which would reduce effects of intraspecific competition on habitat use. Thus, the habitat associations found in my study are likely affected by factors such as food abundance, cover and moisture and are not strongly mediated by biotic interactions such as predation or inter- and intraspecific competition.

Table 1.1. Habitat features used in the multiple regression analysis. Fig. 1.5 illustrates the various sampling plots used.

Features	Description
total trees	Total number trees (DBH $\geq$ 8 cm) within 0.04 ha circular plot.
total saplings	Total number saplings (DBH $<$ 8 cm) within 0.008 ha circular plot.
CWD	Total area covered by down wood ($\geq$ 7 cm diameter) for four 12.5 m transects.
litter depth	Average litter depth from the top of the forest floor to the mineral soil, measured to the nearest cm. If mineral soil was absent, it was measured from the top of the forest floor to a depth where litter was no longer recognizable. Measured once along each of the four transects.
% clay	Percent of clay in the soil, using the ribbon, taste, feel and shine test (Anon 1994) on the first mineral layer. Organic soils were given a value of zero.
soil pH	Measured using the E.W. SYSTEM SOIL TESTER®pH meter. PH was converted to hydrogen ion concentration for the analysis.
slope	Gradient measured in percent, using a clinometer across the 0.04 ha plot in the direction of greatest slope.
aspect	Direction in degrees that the slope was facing. All directions greater than 180 degrees were converted to the mirror image.
seep	Distance from array to nearest source of open water ie. creek, pond, Measured in metres.
% conifer	% conifer species within 0.04 ha plot.
DBH > 26 cm	Number of trees with DBH > 26 cm within 0.04 ha plot.
shrub cover	Average % shrub cover in twelve 1 m^2 quadrates located along the four transects.
herb cover	Average % herb cover in twelve 1 m^2 quadrates located along the four transects. Herb cover included all nonwoody plants, grasses, sedges, and horsetails.
moss cover	Average % moss cover in twelve 1 m^2 quadrates located along the four transects.
distance	Distance from array to pond. Measured in metres.

Table 1.2. Recapture information for six individuals of *Ambystoma macrodactylum* caught at different arrays. Distance was measured as a straight line between array of first and subsequent capture site. Recaptures in 1995 could not be individually identified and therefore the date of initial capture could not be determined.

Pond	Initial Capture	Recapture	Distance	Direction
1	13 Aug. 1994	17 Aug 1994	135 m	toward pond
2	21 Aug. 1994	26 Aug. 1994	135 m	toward pond
3	29 July 1994	21 April 1995	525 m	opposite side of pond
2	?	22 July 1995	315 m	toward pond
1	?	17 Aug. 1995	135 m	away from pond
2	?	23 Aug. 1995	270 m	away from pond

Table 1.3. ANCOVA testing whether total adult captures per 100 trap nights were the same at all arrays. Sum of squares for the effect of array were adjusted for effects of distance from pond and population.

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F	P
COVARIATE					
distance (m)	1	8.7	8.7	7.4	0.013
EFFECTS					
array	5	30.7	6.1	5.2	0.003
population	3	64.0	21.3	18.1	0.000
TWO-WAY INTERACTIONS					
array x population	15	39.7	2.6	2.2	0.044
EXPLAINED	24	134.9	5.6	4.8	0.000
RESIDUAL	21	24.8	1.2		
TOTAL	45	159.6	3.5		

Table 1.4. Variation found for the habitat features used in the multiple regression analysis. Explanation of the habitat features are in Table 1.1.

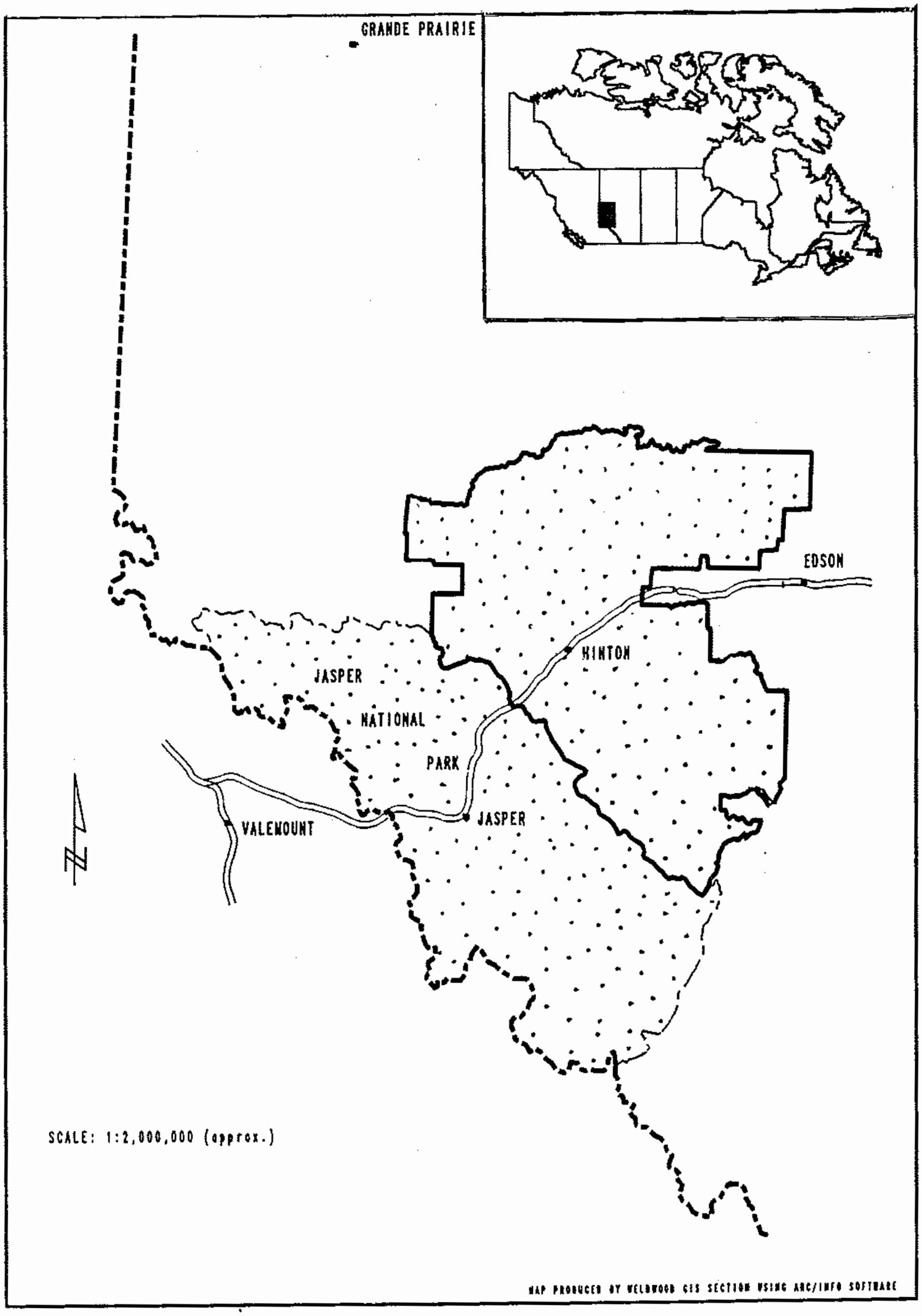
Pond	Habitat Feature	Mean ± S.E.	Habitat Feature	Mean ± S.E.
1	total trees	57 ± 4.8	seep (m)	245 ± 35.1
2		58 ± 10.1		128 ± 66.9
3		39 ± 8.4		73 ± 18.4
4		22 ± 4.4		116 ± 19.5
1	total saplings	17 ± 3.1	% conifer	66 ± 8.3
2		32 ± 5.9		77 ± 9.8
3		34 ± 9.4		71 ± 11.0
4		50 ± 13.0		86 ± 6.7
1	CWD (m^2)	9.2 ± 2.62	DBH > 26 cm	10 ± 1.4
2		3.6 ± 1.12		1 ± 0.3
3		0.1 ± 0.05		2 ± 0.6
4		8.1 ± 2.43		1 ± 0.1
1	litter depth (cm)	9.0 ± 0.50	shrub cover (%)	14 ± 1.4
2		9.2 ± 1.17		23 ± 1.9
3		4.7 ± 0.52		10 ± 1.5
4		3.5 ± 0.40		20 ± 1.9
1	% clay	21 ± 3.5	herb cover (%)	36 ± 2.9
2		22 ± 5.8		37 ± 5.7
3		35 ± 4.4		38 ± 8.1
4		40 ± 2.3		25 ± 3.0
1	soil pH	6.7 ± 0.06	moss cover (%)	45 ± 6.0
2		6.7 ± 0.04		41 ± 10.7
3		6.8 ± 0.03		62 ± 7.4
4		6.8 ± 0.04		21 ± 5.0
1	slope (%)	10.9 ± 1.62	distance (m)	245 ± 35.1
2		6.1 ± 1.04		244 ± 36.2
3		9.5 ± 1.87		287 ± 22.8
4		9.2 ± 1.17		216 ± 24.5
1	aspect	80 ± 12.9		
2		135 ± 13.5		
3		128 ± 5.1		
4		112 ± 14.2		

Table 1.5. Multiple regression results which examined whether relative abundance of adult long-toed salamanders was associated with the habitat features shown in Table 1.1. The r^2 value was 0.62.

	Degrees of Freedom	Sum of Squares	Mean Square	F value	P
Regression	4	166.6	41.7	20.9	<0.000
Residual	51	101.9	2.0		

Table 1.6. Significant variables found in the multiple regression analysis.

Variable	Coefficient	P
Dummy variable representing Pond 2	2.880	<0.0000
Litter depth (cm)	0.139	0.0235
Distance from pond (m)	-0.004	0.0140
Slope (m)	0.134	0.0010
Y-intercept	2.626	0.0003



MAP PRODUCED BY WELDWOOD GIS SECTION USING ARC/INFO SOFTWARE

Figure 1.1. Location of the Foothills Model Forest in West Central Alberta, Canada as indicated by the stipples.

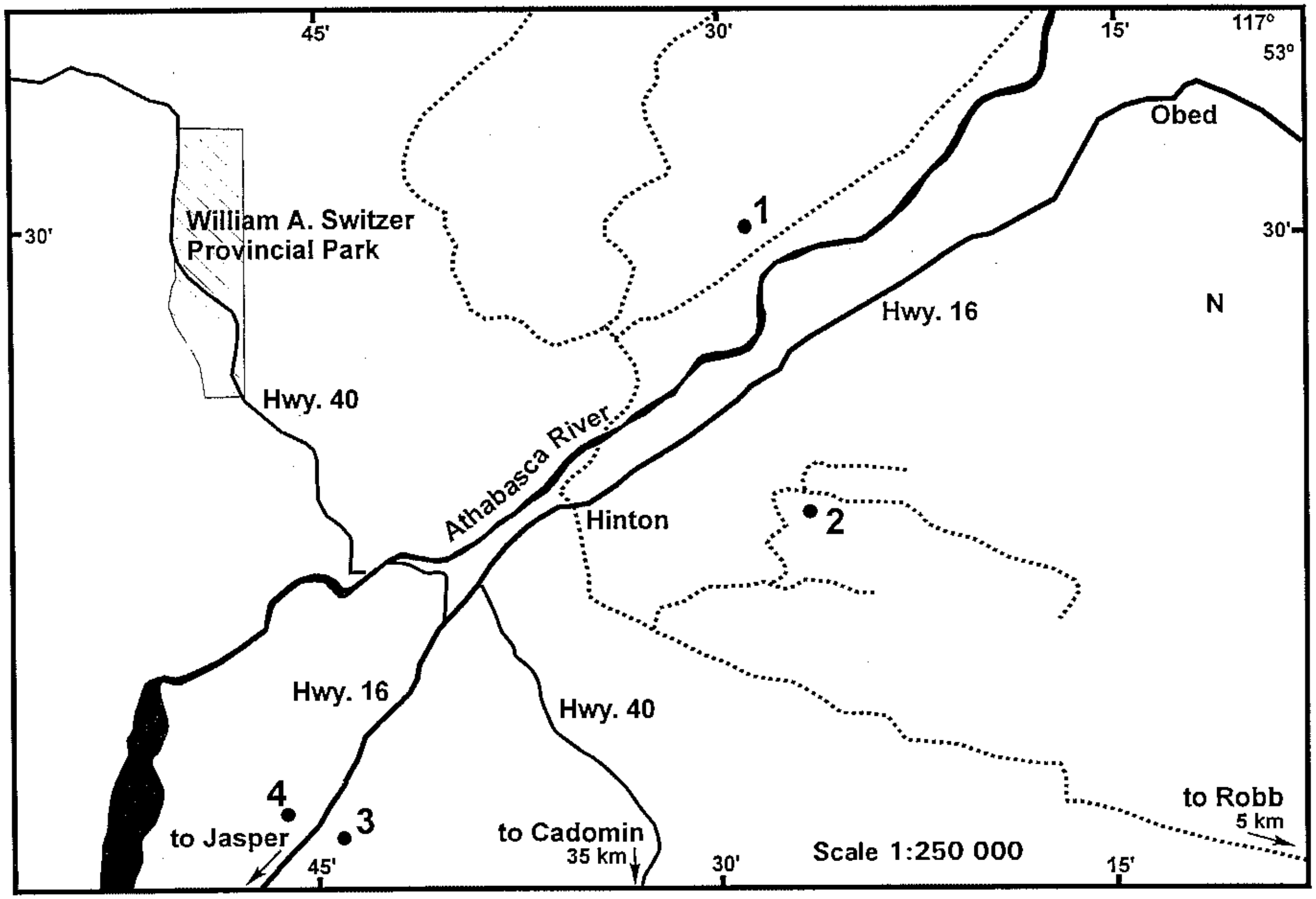


Figure 1.2. Location of the four breeding ponds used to examine habitat features associated with long-toed salamander abundance. Specific pond locations and descriptions are given in Table 2.1. Solid lines represent highways, dotted lines represent logging roads.

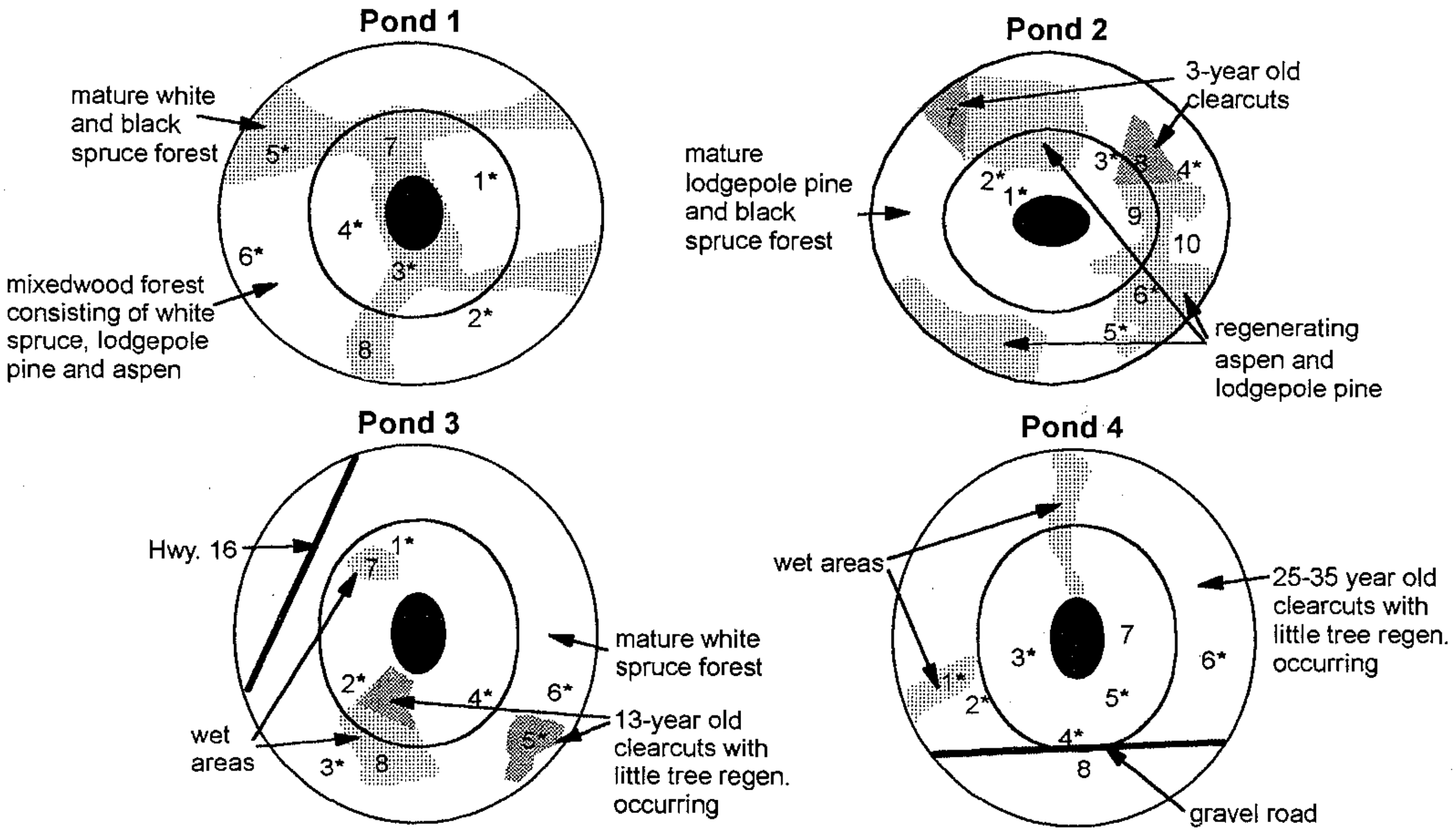


Figure 1.3. Schematic diagram of the four study ponds. The numbers with the asterisks indicate the location of the randomly placed arrays installed during the spring of 1994. The remaining numbers indicate the location of arrays installed during the spring of 1995. The first ring around the pond is 250 m from the pond and the outer ring is 500 m from the pond. The ponds are not drawn to scale.

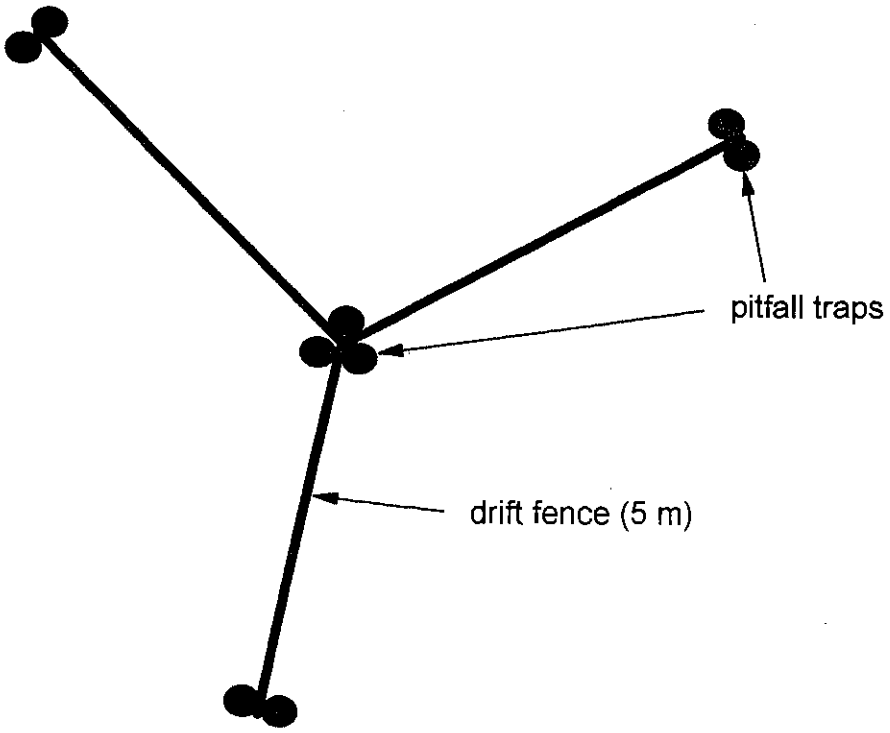


Figure 1.4. Schematic diagram of a pitfall array used to trap salamanders.

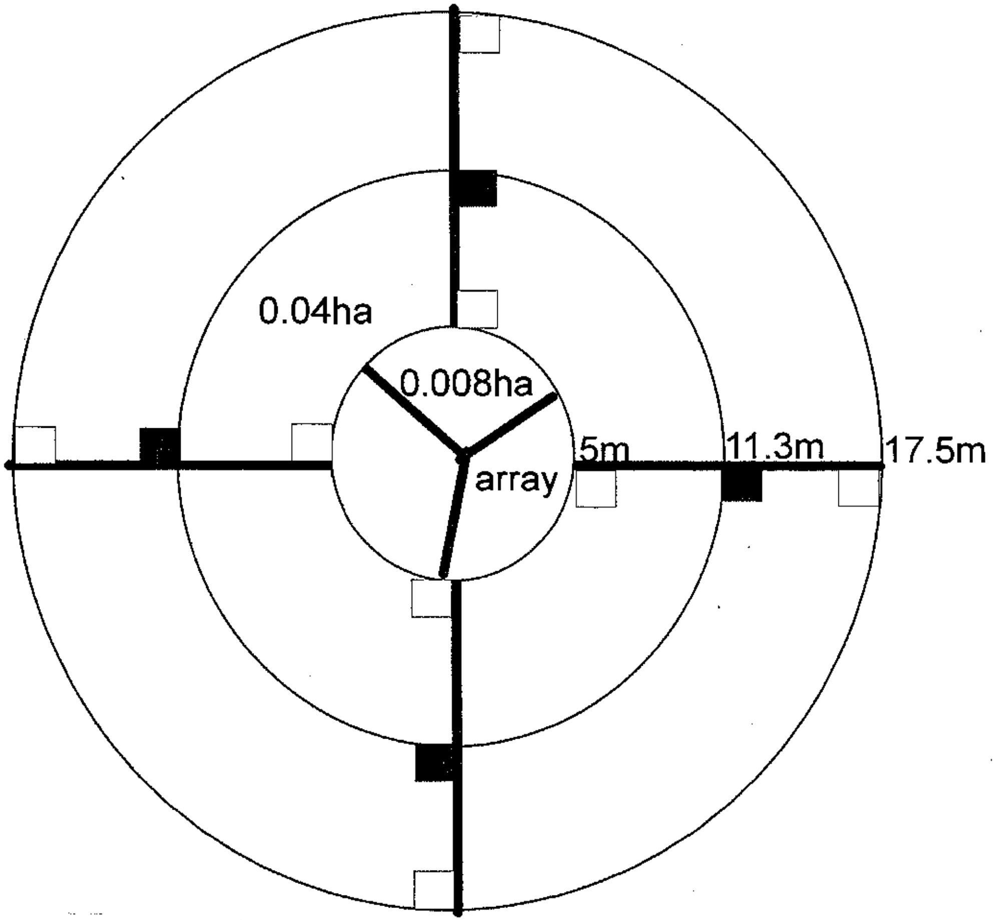


Figure 1.5. Schematic diagram illustrating the vegetation plot used to quantify habitat characteristics. Squares indicate the locations where a $1m^2$ quadrate was used to estimate percent cover. Filled squares were where litter depth was also measured. Downed wood was measured along the four transects. Trees were counted within the 0.04 ha plot and saplings were counted within the 0.008 ha plot.

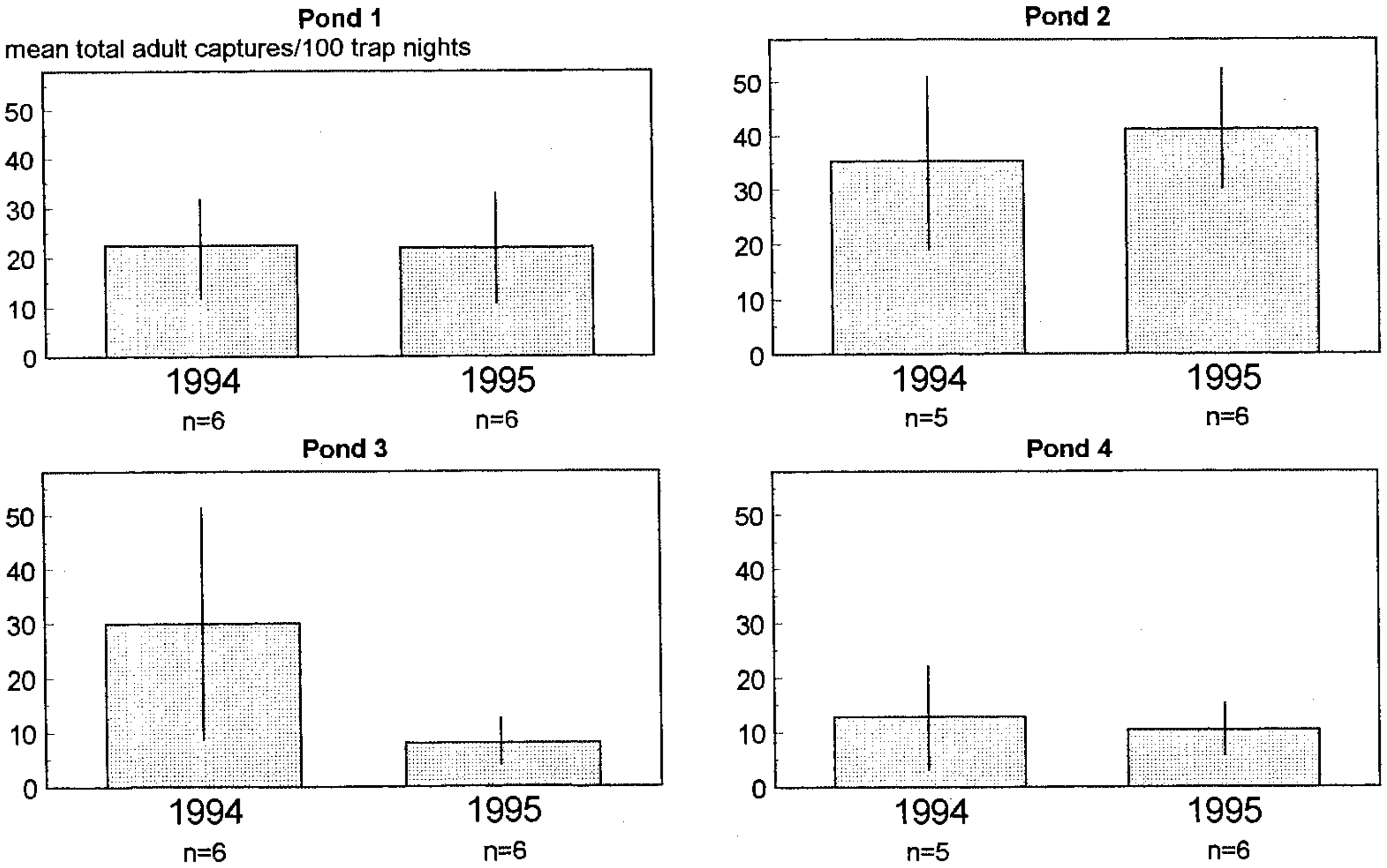


Figure 1.6. A comparison of the total adult salamanders per 100 trap nights caught during 1994 and 1995, averaged over (n) arrays for each study population. Adults were considered as having a snout-vent length > 40 mm. Standard error bars are included.

CHAPTER 2

HABITAT USE OF LONG-TOED SALAMANDERS AT A MACROHABITAT AND LANDSCAPE SCALE

INTRODUCTION

In Chapter 1, specific features of the terrestrial habitat explained some of the variation in abundance of adult long-toed salamanders, which suggested that individuals chose sites with specific habitat features when establishing summer home ranges. However, it is not known whether individuals are associated with a specific habitat type in which they will subsequently set up their summer home range or whether populations are associated with a certain landscape within which they will subsequently live and reproduce. In this chapter, habitat use at a macrohabitat and landscape scale are examined to determine whether salamanders are using habitats at these scales differently. For both scales, I use relative abundance as a index of habitat use.

I first compare relative abundance of adult salamanders across the different habitat types found around the breeding ponds in the study area. The study area is part of an active forest management area and the prevalent habitat types are clearcut and forested areas. Past studies have shown that logging may detrimentally affect the abundance of some salamander species. Pough et al. (1987) found fewer red-backed salamanders (*Plethodon cinereus*) in a 7-year old clearcut compared with the adjacent forest. Most terrestrial salamander species were either eliminated or reduced in numbers in recent clearcuts (less than five years old) compared with mature forest (Petranka et al. 1994). Similarly, most salamander species were adversely affected by timber removal in clearcuts that were less than 10 years old (Petranka et al. 1993). It is unknown whether long-toed salamanders are found in similar numbers in forested habitats compared with clearcuts. In this chapter, I examine whether the relative abundance of long-toed salamanders differ between clearcuts and forested areas.

Research has indicated that amphibian species respond differently to different moisture regimes. Some species such as roughskin newts, *Taricha granulosa* (Aubry and Hall 1991), ensatinas, *Ensatina eschscholtzii* (Aubry and Hall 1991, Bury et al. 1991) and north-western salamanders, *Ambystoma gracile* (Aubry and Hall 1991), were associated with well drained sites whereas other species like the tailed frog, *Ascaphus truei,* were more commonly found on wet poorly drained sites (Corn and Bury 1991, Aubry and Hall 1991). Wet areas are often left undisturbed during logging operations because few harvestable trees grow there. If harvesting is detrimental to the terrestrial life stage of long-toed salamanders, these areas could provide refuges for adults during the summer. In this chapter, I compare the relative abundance of long-toed salamanders in wet, poorly drained sites with dry, well drained sites.

Lastly, I am interested in determining whether larger salamander populations are associated with landscapes that have little to no harvested areas compared with landscapes with large harvested areas (i.e. were more salamanders using unharvested landscapes compared with harvested landscapes). I use the relative abundance of eggs in ponds to infer whether the size of breeding populations are associated with the amount of harvesting that had occurred in the surrounding landscape.

MATERIALS AND METHODS

Relative Abundance in Different Habitat Types

To determine whether relative abundance of adults differed in clearcut areas compared with forested areas, adult captures were compared using four arrays located in the centre of clearcuts and four arrays located in forested areas. All arrays in clearcuts were at least 25 m from the forest edge. Clearcut areas were all cut and scarified before 1982 and all forested sites were at least 80 years old.

Four pairs of forested areas and clearcut areas were compared. Each pair were at similar distances (not exceeding 500 m) from the breeding pond and had similar pre-harvest forest types. Two pairs were located around Pond 2 (Fig 1.3; array 5 with 7 and array 4 with 8 were the forested area paired with the clearcut area respectively). One forested area and one clearcut area were located at Pond 3 (Fig 1.3; array 5 with 6 respectively) and one forested area and one clearcut area were located at Pond 5 (Fig. 2.1). Location of all ponds are shown in Figure 2.2 and a description is given in Table 2.1).

Arrays were in place from the beginning of June 1995 to the end of August 1995. All salamanders were measured, marked and released using the same method as described in Chapter 1. The total number of salamanders captured over the summer was converted to total adult captures/100 trap nights. Salamanders greater than 4.0 cm SVL were considered to be adults.

A similar design was used to compare captures in wet areas with forested areas. Wet areas were defined as areas having the top layer of soil saturated but did not have standing water present for the majority of the summer. These areas were dominated by sedges, scattered bog birch and in one case some stunted white spruce (Pond 4, array 1). In addition, the ground had to be solid enough so that salamanders could not get underneath the fences of the array. Three pairs of arrays in wet areas and forested areas were compared. Two pairs were located around Pond 3 (Fig. 1.3; array 1 with 7 and array 3 with 8 were the forested area paired with the wet area respectively) and one pair was located at Pond 4 (Fig. 1.3; array 2 was the forested area and array 1 was the wet area). All arrays in wet areas were at least 20 m from the forest edge.

Paired sample t-tests were use to compare captures. The power and the sample sizes needed to detect if a statistical difference existed between the comparisons were also determined (Zar 1984).

Sizes of Breeding Populations at Different Ponds

Topographic maps and aerial photographs were used to find potential breeding ponds in the vicinity of Hinton during the spring of 1994 and 1995. All types of water bodies were examined for eggs but only ponds that were permanent and fishless were used in this study. Ponds were determined to be fishless by visual observation and confirmation by fishermen and biologists familiar with area. Habitat alterations within 500 m of the breeding ponds were only forestry or seismic related in the form of clearcuts or seismic lines. The egg stage was used as a confirmation of breeding activity of the salamanders because eggs were easily seen during daylight hours by walking along the periphery of the pond. Larvae were much more difficult to see because they hid in the bottom substrate during the day and terrestrial adults were almost impossible to locate without pitfall traps.

Twelve breeding ponds were chosen based on the above criteria. Between May 13 and June 9 1995, egg counts were conducted to provide an estimate of the relative abundance of eggs and hence a relative estimate of the size of the breeding population. To provide the most precise and comparable estimate of relative abundance, eggs were counted at a time when egg laying was just finishing and hatching was just beginning. This was determined by examining the stage of the eggs to see how many were newly laid and how many were close to hatching. Sometimes, it was difficult to judge the best time for conducting egg counts so egg counts at some ponds were repeated 3 to 5 days later and the maximum estimate was used.

Egg counts consisted of walking 10-m transects placed randomly along the shore of each pond and counting all salamander eggs within 2 m of the shoreline. Long-toed salamanders lay eggs singly or in small clumps so individual eggs were counted. Four to six transects were done for each pond, depending on the size of the pond. Inner pond transects were conducted using a dingy. This involved counting the number of eggs within a 1-m width strip, beginning 2 m from the shore and moving toward the centre of the pond until no more eggs were observed. The maximum distance that eggs were observed from shore was also recorded. Two to four transects were conducted for each pond, depending on the size of the pond. A floating piece of clear plastic was used to improve visibility through the water column. Transects were not used to estimate the number of eggs in Ponds 7 and 12 because they were small enough that counting all the eggs was possible.

The data from the shoreline transects were used to calculate the mean number of eggs/m^2 for the outer 2 m of the pond. The area of the outer 2 m of the pond was determined and an estimate of the number of eggs in the outer 2 m of the pond was calculated by multiplying the mean number of eggs/m^2 with that area. A similar method was used to estimate the number of eggs in the area that was surveyed using the dingy, i.e., the area 2 m from the shore to the maximum distance that eggs were no longer found. The total number of eggs calculated from both the shoreline and the inner pond transects were added together to give the total number of eggs estimated for that pond.

To determine whether the number of eggs laid were consistent among females, an attempt was made to get several females to lay eggs in buckets. Females were caught en route to the pond in the early spring using drift fences or were caught at night in the pond during amplexus to ensure that only females that had not begun egg laying were used. The female, a male, and some twigs were put into a bucket filled half full with pond water. The buckets were left in the field adjacent to the breeding pond. I assumed that egg laying was over when no further eggs were produced after one week and the body of the female was no longer swollen. Eggs were counted, the snout-vent length of the female was measured. Both adults and the eggs were placed back in the pond.

To test whether egg abundance was associated with the harvested area around the ponds, the total number of eggs at each pond was regressed with the total harvested area around the ponds. I also included in the analysis the total surface area of each pond and the number of years since the first harvest. The total area of the pond was included in the regression analysis to remove any effect the size of the pond had on the relative abundance of eggs. Because the time of harvesting ranged from 1957 to 1992, the number of years since the first harvest was included in the analysis to potentially reveal the time it takes for the size of populations to recover to a similar size as undisturbed populations (if harvesting is detrimental to populations). Because I did not know the maximum distance that clearcuts could be from the pond and still potentially impact the populations, I did two separate regression analyses. The first used the area of clearcuts within 250 m of the breeding ponds and the second used the area of clearcuts within 500 m of the breeding ponds.

RESULTS

Relative Abundance in Different Habitat Types

Captures in clearcuts compared with the nearby forest are shown in Figure 2.3. Captures in wet areas compared with the adjacent forest are also shown in Figure 2.3. There were no significant differences between captures in clearcut and forested areas (paired sample t-test, $n = 4$, $P > 0.05$) or between wet areas and forested areas (paired sample t-test, $n = 3$, $P > 0.05$) but small sample sizes reduced the power of these tests and gave a 50% probability of committing a Type II error. An a posteriori power analysis revealed a minimum sample size of seven pairs (i.e., seven arrays in clearcut areas and seven arrays in forested areas) would be needed to determine whether there was a significant difference of at least 10 salamanders captured between clearcut and forested areas at an alpha level of 0.05 and a power of 0.10. Similarly, a minimum sample size of six pairs would be needed to detect a difference of 10 salamanders captured when comparing between wet areas and forested areas.

Breeding Populations at Different Ponds

The only breeding ponds located in the Foothills Model Forest, after searching an area ranging from Cadomin to the south, William A. Switzer Provincial Park to the north and Obed to the east, were predominantly within the Athabasca River drainage or in the headwaters of the McCleod River drainage close to the divide between the Athabasca and McCleod River systems. Breeding ponds were found in all types of water bodies, including beaver ponds, roadside ditches, ephemeral ponds, and large permanent ponds. Ponds with fish tended to have relatively few if any eggs. All fishless ponds examined that were within the long-toed salamanders' range had eggs present. Locations of the 12 breeding ponds selected for the analyses are shown in Fig. 2.2.

The 12 ponds varied considerably in size (Table 2.1), however every pond tended to have large areas where water depth was less than 1 m. This appeared to be an important area as eggs were only found at depths less than 1 m. Eggs were easily visible and were always found on some sort of vegetation, such as live and dead sticks, horsetails, or lily pads.

A total of eight salamanders (4 males and 4 females) were captured and used to determine the number of eggs laid by females. Two pairs were from pond 1 and two pairs were from pond 3. The mean number of eggs/female was 220.75 and the standard error was 4.37 (Table 2.2).

The age and area of harvesting around the 12 ponds varied considerably (Figure 2.4). Two ponds did not have any harvesting associated with them (Ponds 1 and 6) and three ponds had greater than 65% of the area harvested (Ponds 4, 8 and 11). Harvested areas older than 1980 were most abundant, and cuts created during the 1980's and 1990's were less abundant, respectively.

The regression analyses are shown in Tables 2.3 and 2.4. Harvested areas around breeding ponds, both within 250 m and 500 m from the ponds, were not associated with the relative abundance of eggs nor was time since the first clearcut associated with the relative abundance of eggs. The area of the pond was significantly associated with the number of eggs in both tests, indicating that the larger the pond, the larger the breeding population (Table 2.4).

DISCUSSION

No conclusions could be drawn from the comparison of relative abundance of individuals in clearcut areas versus forested areas. This resulted from the low power of the test caused by a large variation in relative abundance within similar habitat types among the populations sampled. Although the comparison between wet areas and forested areas was also inconclusive because of low power, I suspect that long-toed salamanders do use wet areas less than forested areas. Because the long-toed salamander cannot effectively burrow on its own (Semlitsch 1983), it relies on small mammal burrows or natural crevices for cover (Semlitsch 1981). The common small mammals in the area are masked shrews (*Sorex cinereus*), dusky shrews (*Sorex monticolus*), red-backed voles (*Clethrionomys gapperi*) and deer mice (*Peromyscus maniculatus*) (Smith 1993). Although shrews are considered a predator of amphibians, Ambystomatid salamanders have a noxious secretion that shrews find unpalatable (Brodie et al. 1979) and may therefore leave long-toed salamanders alone. None of the small mammal species in the area are likely to build subterranean burrows in water saturated ground. Furthermore, the wet areas did not have any large trees or rocky debris that provided natural crevices. The lack of adequate cover in these wet areas probably restrict the use of these areas by long-toed salamanders.

The amount of harvesting within 500 m or 250 m of breeding ponds was not associated with the relative abundance of eggs (i.e. the size of the breeding population). This suggests that harvesting in the vicinity of breeding ponds does not affect either the survival of adults throughout the summer or their use of these ponds for breeding. This is in contrast with past work where alterations associated with harvesting did impact populations of Ambystomatid species. Clearcuts and the subsequent conversion of longleaf pine species to slash pine plantations essentially eliminated a population of flatwoods salamanders *Ambystoma cingulatum* (Means et al. 1996), however, it was not clear in that study whether harvesting impacted reproductive success, terrestrial survivorship or both.

Tree harvesting in the vicinity of aquatic systems may detrimentally affect the breeding habitat by causing an increase in siltation rates which may degrade larval habitat (Corn and Bury 1989, deMaynadier and Hunter 1995) and reduce reproductive success. Although I did not directly measure reproductive success, my results suggest that harvesting proximate to breeding ponds did not significantly impact reproductive success. Based on the data collected on four breeding females, the number of eggs laid per female appears to be fairly consistent and is likely not a determinant factor on population size. Larval survival could have a large influence on population size, as this stage is most vulnerable to predation and desiccation (Woodward and Mitchell 1991), however, the fate of the eggs was not followed through to hatching and emergence of juveniles. Nonetheless, if a reduction in reproductive success was associated with an increase in harvesting around a pond, a reduction in population size should eventually occur if immigration is low. Low immigration is reasonable because species in the genus *Ambystoma* are thought to be philopatric so few individuals are likely to stray from their natal pond.

Harvesting around a breeding pond has been shown to cause individuals of some Ambystomatid species to move away from clearcuts or perhaps cause some individuals to die. Forest harvesting 156 m from a breeding pond was suggested as causing a change in migratory movements and an increase in mortality of mole salamanders *Ambystoma talpoideum* on the clearcut side of the pond (Raymond and Hardy 1991). If an increase in terrestrial mortality of long-toed salamanders occurred because of harvesting in my study, the mortality rate appears to be low enough to not have a significant impact on population size.

There was no association between time of first cut and population size in my study. In contrast, several studies in eastern North America which examined the abundance of red-backed salamanders (*Plethodon cinereus*) in different aged forests found that red-backed salamanders reached predisturbance levels in clearcuts after 30-60 years (Pough et a. 1987, DeGraaf and Yamasaki 1992, Petranka et al. 1993). Amphibian populations in northern Florida were seen to recover by the third year after harvesting (Enge and Marion 1986). If populations of long-toed salamanders were detrimentally affected by harvesting in the first few years and then recovered as the forest grew back, I would have expected to see smaller populations of salamanders at ponds with recently harvested areas and larger populations at ponds with regenerating areas. The small number of ponds with clearcuts less than five years old likely did not provide the power necessary to reveal this result if a negative effect occurred on populations within the first five years. Nonetheless, given enough time populations living in harvested landscapes do not seem to be any different in size compared with populations living in relatively undisturbed landscapes, albeit I do not know whether the populations recovered to their predisturbance sizes.

Although the amount of harvesting in the area was not associated with the relative abundance of eggs, the surface area of the ponds was significantly associated with egg abundance. Large ponds tended to support large breeding populations as indexed by egg counts. This is likely a function of large ponds having more egg laying substrate available, more food and cover available for the larvae throughout the summer, easier to locate during spring migration and less likely to dry up in exceptionally dry summers.

Whether the founding individuals actively selected large ponds or this association is a result of differential survival is not known. I suspect that long-toed salamanders are not very selective in their choice of ponds for breeding because long-toed salamander eggs were found in all types of water bodies, including roadside ditches, beaver ponds, and ephemeral ponds (Hamilton et al. 1996). Because this salamander species is considered philopatric, individuals are thought to return to their natal pond to breed and unlikely to move to a different pond if their natal pond becomes unsuitable for reproduction. The fact that large ponds had large breeding populations may be a result of large ponds having a greater chance of being discovered by the first breeding individuals that did not return to the natal pond and large ponds could have a better chance of maintaining a viable population compared with small or ephemeral ponds that periodically dry up.

My results suggest that long-toed salamanders do not use landscapes with large harvested areas any more or less than landscapes with little harvesting and indicates that long-toed salamanders are generalists at this scale with respect to harvesting.

Table 2.1. Location of *Ambystoma macrodactylum* breeding ponds and the total number of eggs estimated to be in each pond. Map refers to topographic maps produced by Canadian Department of Energy, Mines and Resources. Localities are shown in Fig 2.2. Ponds 1-4 are the ponds referred to in Chapter 1. The egg laying area is the area of the pond that was 1 m in depth or less.

Pond	Map	UTM Coord.	Lat./Long.	Elevation(m)	Surface Area (ha)	Total Eggs	Egg Laying Area (m²)
1	83F/6	11U MK 678 279	53°30'00"/117°30'00"	1150	1.3	23 741	2997
2	83F/6	11U MK 715 167	53°24'00"/117°25'45"	1260	5	185 199	6995
3	83F/5	11U MK 523 043	53°17'45"/117°43'45"	1045	0.8	9 194	1691
4	83F/5	11U MK 495 042	53°17'15"/117°45'30"	1150	2	32 916	6315
5	83F/6	11U MK 720 092	53°20'00"/117°25'15"	1365	3	25 781	2828
6	83F/5	11U MK 604 113	53°21'15"/117°35'45"	1106	1	97 316	2457
7	83F/5	11U MK 654 010	53°15'30"/117°31'15"	1485	0.1	300	100
8	83F/5	11U MK 495 080	53°19'15"/117°45'30"	1170	2	111	2797
9	83F/6	11U MK 685 095	53°20'15"/117°28'45"	1365	2.8	47 823	3721
10	83F/6	11U MK 801 150	53°23'00"/117°17'15"	1200	0.9	25	2169
11	83F/12	11U MK 645 305	53°31'30"/117°32'00"	1470	4.8	32 653	5227
12	83F/6	11U MK 695 152	53°23'15"/117°27'30"	1273	0.5	275	500

Table 2.2. The number of eggs laid and the SVL for four female long-toed salamanders.

Location	number of eggs	SVL (cm)
Pond 3	213	6.1
Pond 3	214	6.9
Pond 1	225	7.5
Pond 1	231	7.2

Table 2.3. Multiple regression results testing for an association between the relative abundance of eggs in ponds with the harvested areas around the ponds, time since first cut, and size of the ponds.

a) area within 250 m of breeding ponds (r^2 = 0.60)

	Degrees of Freedom	Sum of Squares	Means Square	F value	P value
Regression	3	113368.44	37789.48	3.925	0.054
Residual	8	77015.66	9626.96		

b) area within 500 m of breeding ponds (r^2 = 0.57)

	Degrees of Freedom	Sum of Squares	Means Square	F value	P value
Regression	3	108840.55	36280.18	3.559	0.067
Residual	8	81543.56	10192.94		

Table 2.4. Coefficients for the variables used in the multiple regression analyses testing whether egg abundance was associated with the harvested areas around breeding ponds.

a) within 250 m of breeding ponds

Variable	Coefficient	P value
total area cut	-5.07	0.20
area of pond	0.01	0.01
time since first cut	-0.88	0.72
x-intercept	87.12	0.17

a) within 500 m of breeding ponds

Variable	Coefficient	Significance
total area cut	-1.37	0.27
area of pond	0.01	0.01
time since first cut	-0.75	0.78
x-intercept	90.53	0.16

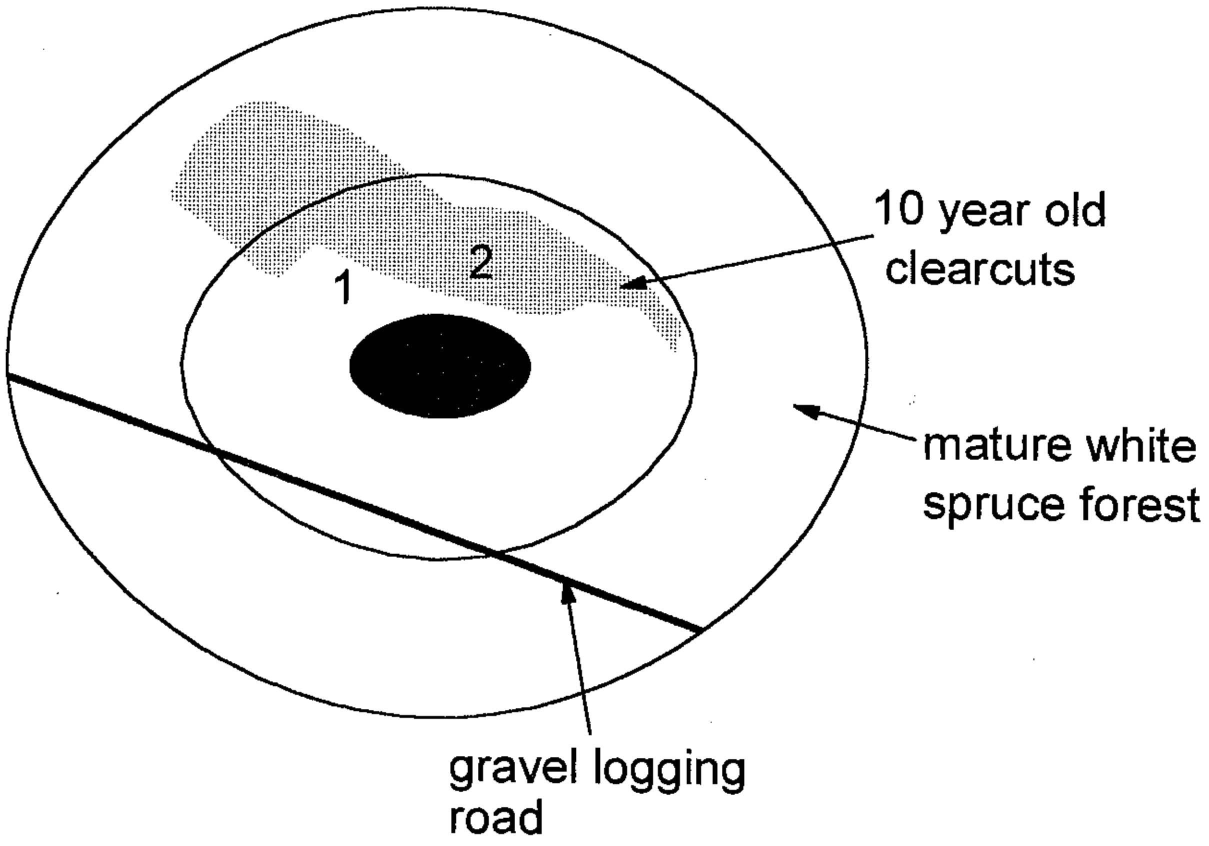


Figure 2.1. Schematic diagram of Pond 5. The numbers indicate the location of arrays installed during the spring of 1995. The first ring around the pond is located at a distance of 250 m from the pond and the outer ring is located at 500 m from the pond. The pond is not drawn to scale. Location of Pond 5 is shown in Fig. 2.2 and a description is given in Table 2.1.

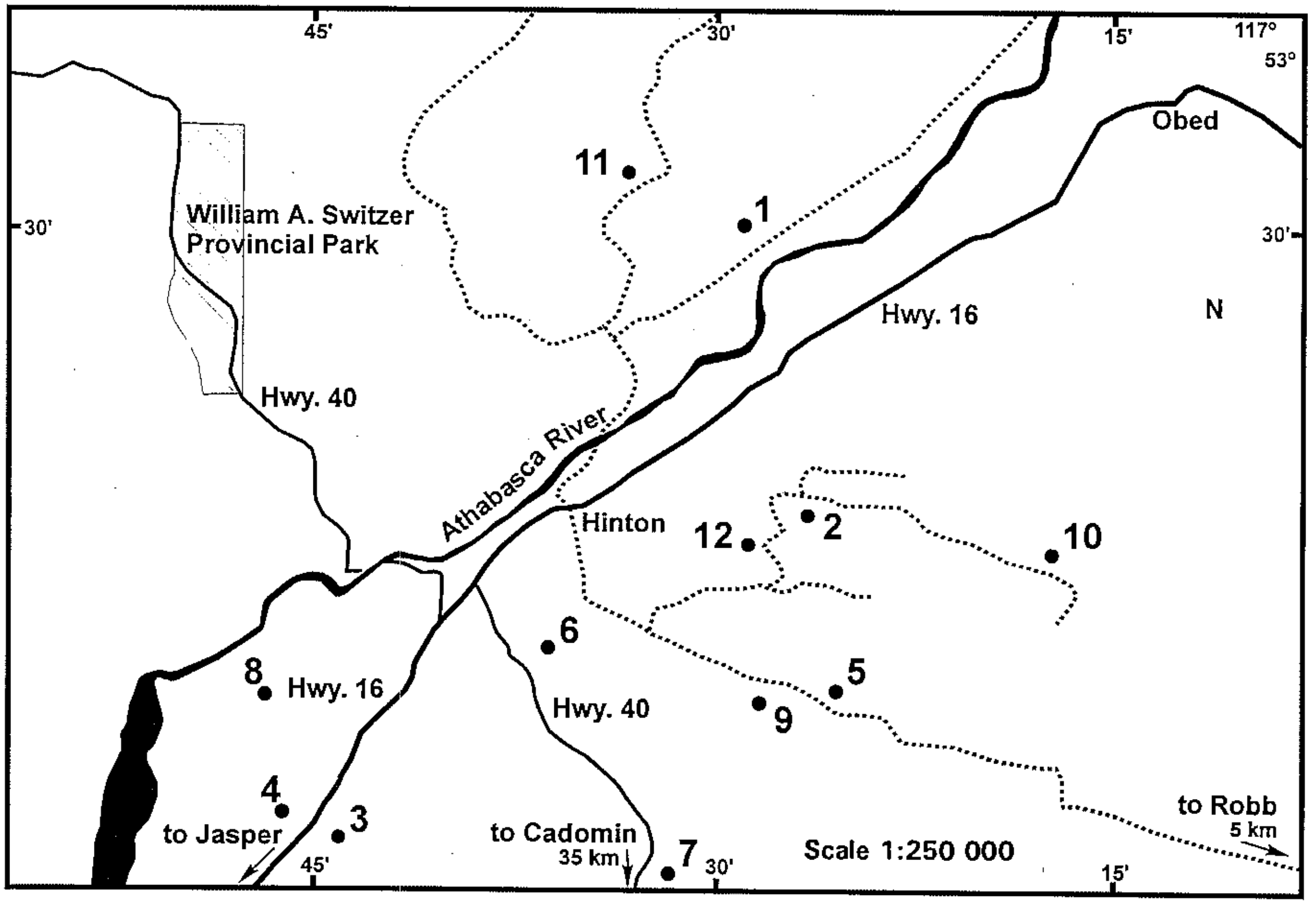


Figure 2.2. Locations of breeding ponds in the Hinton area where terrestrial habitat use was examined. Numbers correspond to pond numbers used throughout text. A description of each pond is given in Table 2.1.

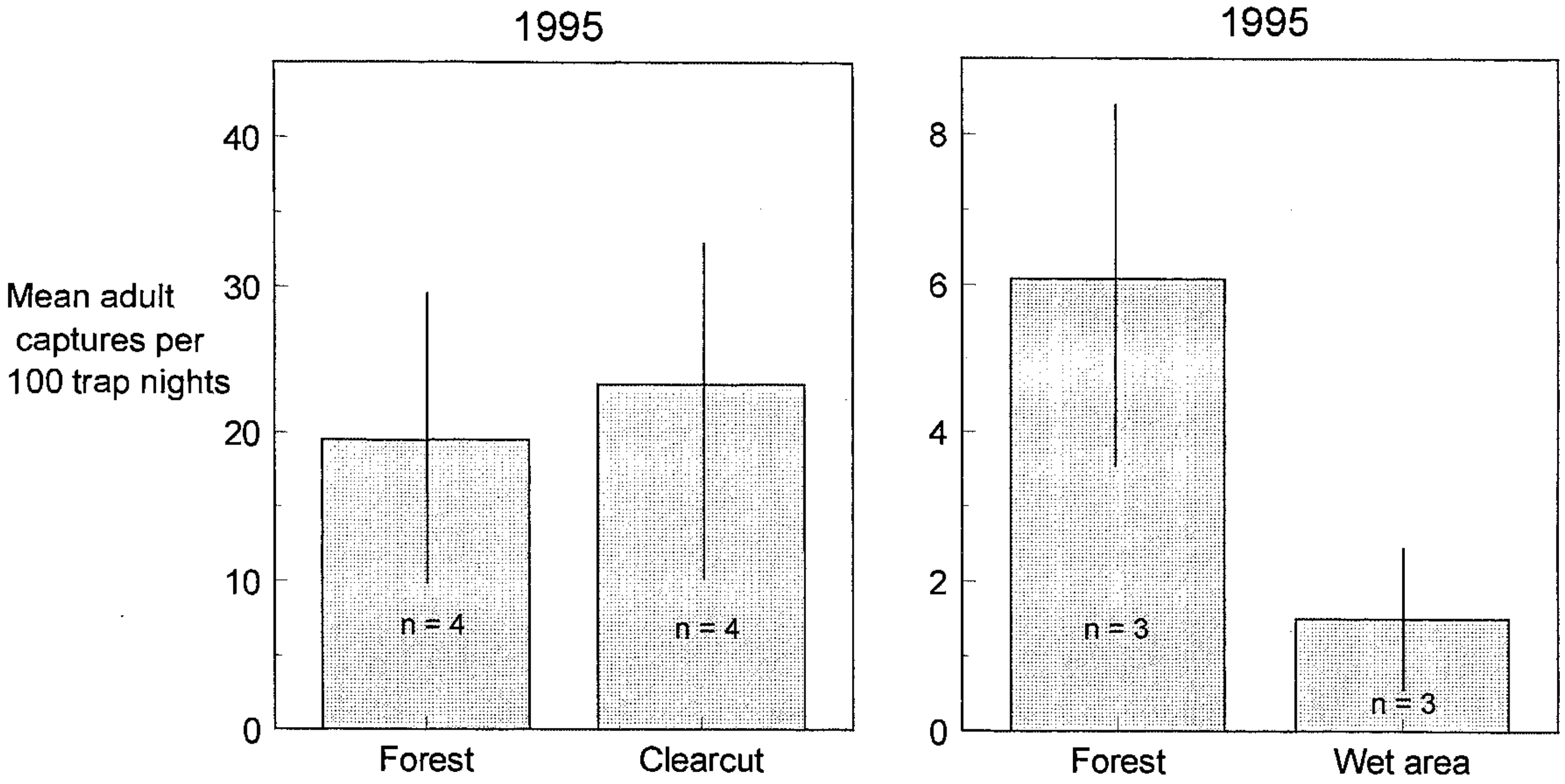
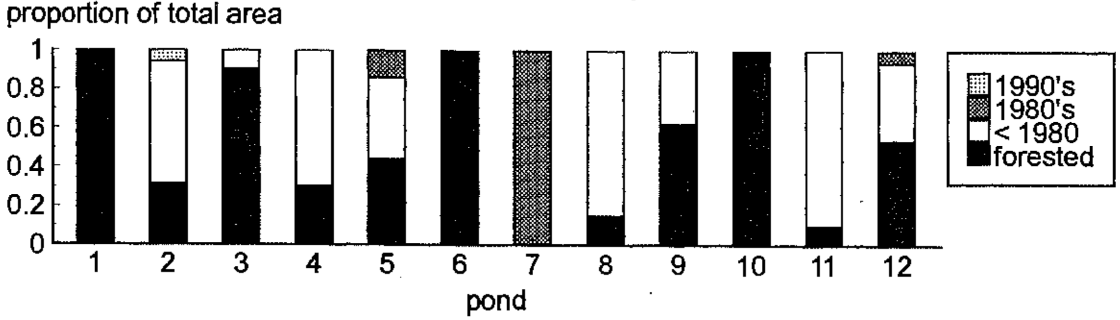


Figure 2.3. A comparison of the total number of adult salamanders captured per 100 trap nights averaged over (n) arrays open during July and August 1995 in forests and adjacent clearcuts and wetlands. Clearcuts ranged from three to thirteen years of age. Wetlands were sites having saturated soil for the majority of the summer. Adults were considered as having a snout-vent length > 40 mm. Standard error bars are included.

a) **within 250 m of pond**



b) **within 500 m of pond**

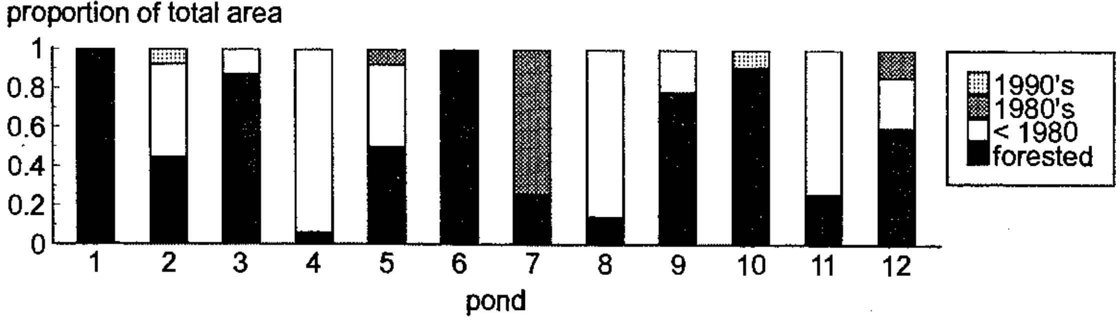


Figure 2.4. Proportion of the various aged clearcuts and forested areas within 250 m (a) and 500 m (b) of the breeding ponds used to examine habitat use at a landscape scale.

GENERAL CONCLUSION

The size of long-toed salamander breeding populations was not associated with harvested or unharvested landscapes. Breeding populations were found in all types of water bodies but large permanent ponds supported larger breeding populations compared with small ponds. Long-toed salamanders appear to be a habitat generalist at this scale.

Whether individuals were selective in the habitat type they chose to live in could not be determined. However, indirect evidence suggested that poorly drained habitats do not support as many individuals as well drained habitats.

Finally, more individuals used sites within habitats that were close to the suspected breeding pond, on a gradient and with a thick litter layer. It is likely that individuals were selecting specific sites within habitats for their summer home ranges.

REFERENCES

Alvarado, R. H. 1967. The significance of grouping on water conservation in *Ambystoma*. Copeia 1967:667-668.

Andrewartha, H. G., and L. C. Birch. 1967. The Distribution and Abundance of Animals. The University of Chicago Press, Chicago and London. 782 pp.

Anonymous. 1991. The Status of Alberta Wildlife. Alberta Forestry, Lands and Wildlife, Fish and Wildlife Division. 49 pp.

Anonymous. 1994. Pre-harvest Ecological Assessment Handbook. Environmental Training Centre, Ref.96, ISBN 0-7732-1411-9, Hinton, Alberta. pp 45.

Aubry, K. B., and P. A. Hall. 1991. Terrestrial amphibian communities in the southern Washington Cascade Range, pp. 327-338. *In* L. F. Ruggiero, K. B. Audry, A. B. Cacey and M. H. Huff (eds.), Wildlife and Vegetation of Unchanged Douglas Fir Forests, U.S. Forest Service Gen. Tech. Rep., Pnw-GTR-285.

Bergin, T. M. 1992. Habitat selection by the western kingbird in western Nebraska: a hierarchical analysis. Condor 94:903-911.

Brodie, E. D., R. T. Nowak, and W. R. Harvey. 1979. The effectiveness of antipredator secretions and behavior of selected salamanders against shrews. Copeia 1979:270-274.

Burton, T. M., and G. E. Likens. 1975. Energy flow and nutrient cycling in salamander populations in the Hubbard Brook experimental forest, New Hampshire. Ecology 56:1068-1080.

Bury, R. B., H. W. Campbell, and N. J. Scott. 1980. Role and importance of nongame wildlife, pp. 197-207. *In* Transactions of the Forty-Fifth North American Wildlife and Natural Resources Conference, Wildlife Management Institute, Washington, D.C.

Bury, R. B., P. S. Corn, and K. B. Aubry. 1991. Regional patterns of terrestrial amphibian communities in Oregon and Washington, pp. 341-350. *In* L. F. Ruggiero, K. B. Aubry, A. B. Cacey and M. H. Huff (eds.), Wildlife and Vegetation of Unchanged Douglas Fir Forests, U.S. Forest Service Gen. Tech. Rep., PNW-GTR-285.

Collins, S. L., and S. M. Glenn. 1991. Importance of spatial and temporal dynamics in species regional abundance and distribution. Ecology 72:654-664.

Corn, P. S., and R. B. Bury. 1989. Logging in western Oregon: response of headwater habitats and stream amphibians. Forest Ecology and Management 29:39-57.

Corn, P. S., and R. B. Bury. 1991. Terrestrial amphibian communities in the Oregon Coast Range, pp. 305-317. *In* L. F. Ruggiero, K. B. Aubry, A. B. Cacey and M. H. Huff (eds.), Wildlife and Vegetation of Unchanged Douglas Fir Forests, U.S. Forest Service Gen. Tech. Rep., PNW-GTR-285.

Crump, M. L., and N. J. Scott. 1994. Visual encounter surveys, pp. 84-92. *in* W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek and M.

S. Foster (eds.), Measuring and Monitoring Biological Diversity. Standard Methods for Amphibians, Smithsonian Institution Press, Washington.

DeGraaf, R. M., and M. Yamasaki. 1992. A nondestructive technique to monitor the relative abundance of terrestrial salamanders. Wildlife Society Bulletin 20:260-264.

deMaynadier, P. G., and M. L. Hunter. 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. Environmental Review 3:230-261.

Diller, L. V., and R. L. Wallace. 1994. Distribution and habitat of *Plethodon elongatus* on managed, young growth forest in north coastal California. Journal of Herpetology 28:310-318.

Douglas, M. E. 1981. A comparative study of topographical orientation in *Ambystoma* (Amphibia: Caudata). Copeia 1981:460-463.

Dueser, R. D., and H. H. Shugart. 1978. Microhabitats in a forest-floor small mammal fauna. Ecology 59:89-98.

Enge, K. M., and R. R. Marion. 1986. Effects of clearcutting and site preparations on herpetofauna of a north Florida flatwoods. Forest Ecology and Management 14:177-192.

Ferguson, D. E. 1961. The geographic variation of *Ambystoma macrodactylum* Baird, with the description of two new subspecies. American Midland Naturalist 65:311-338.

Fraser, D. F. 1976. Empirical evaluation of the hypothesis of food competition in salamander of the genus *Plethodon*. Ecology 57: 459-471.

Gutzwiller, K. J., and S. H. Anderson. 1986. Improving vertebrate-habitat regression models, pp. 161-164. *In* J. Verner, M. L. Morrison and C. J. Ralph (eds.), Wildlife 2000: Modelling Habitat Relationships of Terrestrial Vertebrates, The University of Wisconsin Press, Wisconsin.

Hamilton, I. V., K. L. Graham, L. Powell, and A. Russell. 1996. The range of long-toed salamanders in north western Alberta. Unpublished report submitted to Alberta Forest, Lands and Resource.

Heatwole, H. 1961. Habitat selection and activity of the wood frog, *Rana sylvatica* Le Conte. American Midland Naturalist 66:301-313.

Holomuzki, J. R. 1986. Predator avoidance and diel patterns of microhabitat use by larval tiger salamanders. Ecology 67:737-748.

Jaeger, R. G. 1971. Competition exclusion as a factor influencing the distribution of two species of terrestrial salamanders. Ecology 52:632-637.

Jaeger, R. G. 1980. Fluctuations in prey availability and food limitation for a terrestrial salamander. Oecologia 44:335-341.

Johnson, B. 1991. Habitat loss and declining amphibian populations, pp. 71-75. *In* C. A. Bishop and K. E. Pettit (eds.), Declines in Canadian amphibian populations: Designing a National Monitoring Strategy, Occasional Paper No. 76, Canadian Wildlife Service.

Johnson, D. H. 1981. The use and misuse of statistics in wildlife habitat studies, pp. 11-19. *In* D. E. Capen (ed.), The Use of Multivariate Statistics in Studies of Wildlife Habitat, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Karr, J. R. 1981. Rationale and techniques for sampling avian habitats: Introduction, pp. 26-28. *In* D. E. Capen (ed.), The Use of Multivariate Statistics in Studies of Wildlife Habitat, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Kotliar, N. B., and J. A. Wiens. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59:253-260.

Martin, D. L., R. G. Jaeger, and C. P. Labat. 1986. Territoriality in an *Ambystoma* salamander? Support of the null hypothesis. Copeia 1986:725-730.

McKenzie, D. S., and R. M. Storm. 1970. Patterns of habitat selection in the clouded salamander, *Aneides ferreus* (Cope). Herpetologica 26:450-454.

Means, D. B., J. G. Palis, and M. Baggett. 1996. Effects of slash pine silviculture on a Florida population of flatwoods salamander. Conservation Biology 10:426-437.

Morris, D. W. 1984. Patterns and scale of habitat use in two temperate-zone, small mammal faunas. Canadian Journal of Zoology 62:1540-1547.

Morris, D. W. 1986. Ecological scale and habitat use. Ecology 68:362-369.

Morris, D. W. 1992. Scales and costs of habitat selection in heterogeneous landscapes. Evolutionary Ecology 6:412-432.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1992. Wildlife-habitat Relationships. The University of Wisconsin Press, Madison, Wisconsin. 343 pp.

Noon, B. R. 1981. Techniques for sampling avian habitats, pp. 42-52. *In* D. E. Capen (ed.), The Use of Multivariate Statistics in Studies of Wildlife Habitat, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Orians, G. H., and J. F. Wittenberger. 1991. Spatial and temporal scales in habitat selection. American Naturalist 137 (supplement):s29-s49.

Patton, D. R. 1992. Wildlife Habitat Relationships in Forested Ecosystems. Timber Press, Portland, Oregon. 392 pp.

Petranka, J. W., M. E. Eldridge, and K. E. Haley. 1993. Effects of timber harvesting on southern appalachian salamanders. Conservation Biology 7:363-370.

Petranka, J. W., M. P. Brannon, M. E. Hopey, and C. K. Smith. 1994. Effects of timber harvesting on low elevation populations of southern appalachian salamanders. Forest Ecology and Management 67:135-147.

Pough, F. H. 1983. Amphibians and reptiles as low energy systems, pp.

141-188. *In* W. P. Aspey and S. I. Lustick (eds.), Behavior energetics: the cost of survival in vertebrates, Ohio State University Press, Columbus, Ohio.

Pough, F. H., E. M. Smith, D. H. Rhodes, and A. Collazo. 1987. The abundance of salamanders in forest stands with different histories of disturbance. Forest Ecology and Management 20:1-9.

Raymond, L. R., and L. M. Hardy. 1991. Effects of a clearcut on a population of the mole salamander,(*Ambystoma talpoideum*), in an adjacent unaltered forest. Journal of Herpetology 25:509-512.

Russell, A. P., and A. M. Bauer. 1993. The Amphibians and Reptiles of Alberta. University of Calgary Press, University of Edmonton Press, Calgary and Edmonton, Alberta. 264 pp.

Semlitsch, R. D. 1981. Terrestrial activity and summer home range of the mole salamander (*Ambystoma talpoideum*). Genetics 59:315-322.

Semlitsch, R. D. 1983. Burrowing ability and behavior of salamanders of the genus *Ambystoma*. Genetics 61:616-620.

Sheppard, R. F. 1977. The Ecology and Home Range Movements of *Ambystoma macrodactylum krausei*. M.Sc Thesis, University of Calgary, Calgary, Alberta.

Smith, H. C. 1993. Alberta Mammals: An Atlas and Guide. The Provincial Museum of Alberta. Edmonton, Alberta. 238 pp.

Smith, K. G., and P. G. Connors. 1993. Postbreeding habitat selection by shorebirds, water birds, and land birds at Barrow, Alaska: a multivariate analysis. Genetics 71:1629-1638.

Snedecor, G. W., and W. G. Cochran. 1989. Statistical Methods. Iowa State University Press, Ames, Iowa. 503 pp.

Southerland, M. T. 1986. The effects of variation in streamside habitats on the composition of mountain salamander communities. Copeia 1986:731-741.

Stebbins, R. C. 1985. Western Reptiles and Amphibians. Houghton Mifflin Company, Boston. 336 pp.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

Wake, D. B. 1994. Foreword, pp. xv-xvi. *In* W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek and M. S. Foster (eds.), Measuring and Monitoring Biological Diversity. Standard Methods for Amphibians, Smithsonian Institution Press, Washington and London.

Welsh, H. H. 1990. Relictual amphibians and old-growth forests. Conservation Biology 4:309-319.

Welsh, H. H., and A. J. Lind. 1995. Habitat correlates of the Del Norte salamander, *Plethodon elongatus* (Caudata: Plethodontidae), in northwestern California. Journal of Herpetology 29:198-210.

Whitford, W. G., and A. Vinegar. 1966. Homing, survivorship, and overwintering of larvae in spotted salamanders, *Ambystoma* *maculatum*. Copeia 1966:515-519.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385-397.

Woodward, B. D. and S. L. Mitchell. 1991. The community ecology of desert anurans. pp. 223-248. *In* G. Pollis (ed.), The Ecology of Desert Communities. University of Ariona Press, Tucson, Arizona.

Wyman, R. L., and D. S. Hawksley-Lescault. 1987. Soil acidity affects distribution, behavior, and physiology of the salamander *Plethodon cinereus*. Ecology 68:1819-1827.

Zar, J. H. 1984. Biostatistical Analysis. Prentice Hall, New Jersey. 718 pp.