A MULTIPLE SCALE ANALYSIS OF THE EFFECTS OF LANDSCAPE STRUCTURE ON POPULATIONS OF YELLOW-SPOTTED SALAMANDERS (*AMBYSTOMA MACULATUM*)

by

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Abstract

I examine the effects of landscape structure on the incidence and abundance of yellow-spotted salamanders, *Ambystoma maculatum*, and use these population level responses as indirect measures of movement. Two surveys of breeding populations in ponds located in a heterogeneous landscape were conducted and effects of landscape structure assessed at multiple spatial scales. Landscape structure was quantified as the proportion of forest and the total length of roads surrounding ponds. Additionally, the movement capabilities of juvenile *A. maculatum* in different habitat types was explored.

Through the first survey I show that the proportion of forest influences incidence and density at a small spatial scale (100 m). I conclude that the breeding and post-breeding migration movements are influenced by the amount of forest and identify 15 % forest, within 100 m of the pond, as a threshold amount of forest below which *A. maculatum* cannot persist at a pond. Results from a second survey, which encompassed a greater number of ponds at broader spatial scales, concur with the previous survey for the small scale effects of the proportion of forest, however, there is a significant effect of the proportion of forest at a broad spatial scale (1000 m). This provides indication that populations are spatially structured and that the amount of forest increases the connectivity of the landscape for *A. maculatum*. Also, at small spatial scales the total amount of road has a negative effect on incidence and abundance.

Experimentally I assess the rates of movement of juveniles in forested and field habitat. Results show that juveniles can move faster in field habitat than forest. Finally, I explore the possibilities of harmonic radar as a new technique for tracking juvenile *A. maculatum*.

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General Introduction

Wiens (1995) suggests that there is a need for an increase in the body of theory that deals with the areas of landscape and spatial ecology. There is also a need to operationalize terms within the concepts of spatial pattern and process in order to enable links between theoretical and empirical approaches (Wiens *et al.* 1993) and it is recognized that this may be one of the greatest challenges facing "spatial ecology" (Steinberg and Kareiva 1997). Within the current development of "spatial theory" it is recognized that it is important to adopt a multiple scale approach when considering spatial scale in addressing ecological problems (Turner *et al.* 1992; O'Neill *et al.* 1989; Wiens *et al.* 1993; Wiens 1989; Fahrig 1992). Different patterns emerge at multiple spatial scales (Wiens 1989) and different processes and their associated movement behaviours occur at different spatial scales (Ims 1995). Wiens *et al.* (1993) suggest that the analysis of movement may provide valuable insights into issues of spatial scale because movement is so closely related to landscape structure.

Much landscape and spatial ecology research addresses the question: "does landscape structure affect the persistence of populations?" (Steinberg and Kareiva 1997; Tilman *et al.* 1997). It has been shown that it is through the effects of landscape structure on movement that population level responses are affected by changes in landscape structure (Dunning et al. 1992; Kareiva 1990; Wiens 1997). Movement is important at two different levels; at the individual level it allows animals to access heterogeneously distributed resources, and at the population level it is necessary for the establishment and re-establishment of local populations (Taylor 1997). Also, much of the development of our current conceptual framework of spatially structured populations is due to the increased recognition and understanding of the importance of movement (Taylor 1997).

A landscape can be defined simply as a heterogeneous area (Turner *et al.* 1989), and most habitats are naturally heterogeneous (Wiens 1989). The inherent heterogeneity of a landscape can be changed through natural disturbance or anthropogenic activities such as agriculture, forestry, and urbanization (Taylor and Merriam 1996). Landscape structure provides a theoretical framework within which the effects of heterogeneously distributed resources on individuals and populations can be described and quantified over a range of spatial scales (Taylor 1997). Landscape structure can be defined by considering the types and amounts of resources in a landscape and their spatial distribution - landscape composition and configuration (Dunning *et al.* 1992) and the relative ability of an animal to move between resources - landscape connectivity (Taylor *et al.* 1993) (Taylor and Merriam 1995).

Alteration of habitats within the landscape can result in changes in landscape composition through the elimination of resources entirely, by altering their configuration through the rearrangement of resources, or by affecting connectivity through the alteration of the relative ability of an organism to move between resources (Taylor and Merriam 1996). Changes in landscape structure can result in the subdivision of populations and the formation of smaller, isolated populations (Kareiva 1990; Merriam 1991). This, in turn, can negatively affect the persistence of a local population by increasing the risk of extinction (Kareiva 1990). For many species, movement is the process that mediates the effects of landscape structure on population persistence (Kareiva 1990; Hansson 1991).

The determination of the probability of persistence of a population is dependent upon the scale being examined (Wiens 1989; O'Neill *et al.* 1996; Hecnar and M'Closkey 1997). Hecnar and M'Closkey (1997) determined that the status of the green frog (*Rana clamitans*) is scale dependant, determining that there is persistence at the regional and sub-regional scales despite fluctuations at a small spatial scale. It is difficult to know in advance whether one has identified the appropriate scale for detecting an organisms' response to changes in landscape structure (Turner *et al.* 1989; Kareiva 1990; Wiens 1989). Thus a multiple scale approach where we let the organism and its life history requirements define the scale of importance is necessary in ecological research (Wiens *et al.* 1993; Kareiva 1990; Wiens 1989).

Local populations can be described as a distinct breeding unit (Hanski and Gilpin 1991), where persistence is dependent upon the rate of local extinction (Harisson and Taylor 1997). A local extinction is the disappearance of a population (Hansson 1991) and can be a function of resource quality and the effects of changes in landscape structure on the movements of individuals (Harrison and Taylor 1997). Local populations seldom exist in isolation (Hansson 1991) however, and their persistence is dependent upon the movement of individuals between populations (Hanski and Gilpin 1991; Fahrig and Merriam 1994; Ims 1995). Individual movements enhance the persistence of local populations by enabling individuals to access heterogeneously distributed resources through such processes as migration and foraging (Taylor 1997; Hansson 1991; Merrian and Fahrig 1994). Movement also contributes to the persistence of a network of populations where it helps "connect" local populations (Kareiva 1990) through the colonization, recolonization (Taylor 1997; Pither and Taylor 1998), and "rescuing" of local populations (Sjögren-Gulve 1998a). This network of local populations is called a spatially structured population, where the physical location of the local populations is important and the persistence of these multiple populations is dependent upon movement between populations. There is an increase in the understanding of the importance of the process of movement in spatially structuring populations (Taylor 1997).

Changes in landscape structure can affect the persistence of a local population and a spatially structured population by altering the connectivity of the landscape for an organism (Merriam 1991). Connectivity was initially defined to help conceptualize how dispersal between resources mediates the interaction of changes to the landscape on a network of local populations (Merriam 1991). It can be assessed in terms of how movement prevents the isolation of populations through landscape elements that allow organisms to move among resources (Merriam 1991). Connectivity can be inferred (e.g. Roland and Taylor 1997), modeled, or empirically assessed (e.g. Pither and Taylor 1998) (Taylor 1997).

Currently there is a global concern that amphibian species are declining. However, the extent of these reported declines varies across regions, and within and between species (Wyman 1990). Possible causes of decline include: pollution from pesticides, acid precipitation, increased ultraviolet radiation, climate change, and habitat destruction (Wyman 1990; Blaustein *et al.* 1994; Pechman *et al.* 1991). Blaustein *et al.* (1994) suggest that one of the most important factors causing amphibian declines in industrialized countries is anthropogenic induced habitat fragmentation. For several different species of amphibians, links have been made between population declines and changes in landscape structure, noting in particular, the importance of movement between populations (Wyman 1990; Blaustein *et al.* 1994; Sjögren 1991; Reh and Seitz 1990; Vos and Chardon 1998; Marsh and Pearman 1997).

Research has indicated that the connectivity of the landscape is important in the persistence of spatially structured populations of amphibians (see Sjögren 1991; Laan and Verboon 1990; Vos and Chardon 1998). Changes to landscape structure such as habitat loss and increases in habitat fragmentation may limit amphibian movements and dispersal and could decrease the connectivity of the landscape for amphibian species (Marsh and Pearman 1997; Vos and Chardon 1998).

It has been suggested that many amphibian species are more sensitive and susceptible to changes in landscape structure than other species because of specific movement requirements (Wyman 1990; Blautstein *et al* 1994; Marsh and Pearman 1997; Sjögren-Gulve 1998a; Vos and Chardon 1998). Many amphibian species must migrate between required terrestrial and aquatic habitats, have limited dispersal capabilities, are physiologically constrained by their need for moisture, and show strong site fidelity (Wyman 1990; Blaustein *et al.* 1994; deMaynadier and Hunter 1998; Reh and Seitz 1990). Strong site fidelity in breeding individuals reduces the probability of movement between resources (Wiens *et al.* 1993). Such directed (i.e. non-random) movements would decrease the probability of an individual encountering another population or a new resource, thus decreasing the probability of colonization or recolonization.

In this thesis I examined the effects of landscape structure on populations of yellow-spotted salamanders (*Ambystoma maculatum*) at multiple spatial scales. I determined incidence and abundance of breeding individuals and egg masses and used these as indirect measures of movement because these population level responses are a function of the ability of individuals to access breeding sites. *A. maculatum* is an ideal species for examining the role of the process of movement in mediating the effects of changes in landscape structure on populations of organisms and their persistence. *A. maculatum* (Class Amphibia) exhibit many of the life history characteristics and specific resource and movement requirements that make many amphibian species more susceptible to changes in landscape structure.

They have a bi-phasic life cycle, requiring both terrestrial and aquatic resources (Gilhen 1984) and breeding adults exhibit a high breeding site fidelity (Whiteford and Vinegar 1966; Stenhouse 1985; Whiteford and Vinegar 1966). During breeding migration they move through the landscape, from primarily forested overwintering sites to aquatic breeding sites. They are considered explosive breeders which means that migration to aquatic sites and breeding all occur within a relatively short period of time in comparison to other amphibian species (Gilhen 1984). Movement to breeding sites occurs in the early spring, with males arriving first and depositing spermtaphore in the water, followed shortly after by the females. Aquatic sites used for breeding include permanent or temporary ponds, ephemeral pools, even tire ruts or road side ditches (Gilhen 1984). If aquatic conditions, primarily water temperature, are optimal upon hatching, larval development is rapid, with the juveniles emerging by the late summer (end of August) (Gilhen 1984).

The juveniles spend 2 to 6 years in a terrestrial phase, termed the sub-adult stage, prior to first time breeding (Flageole and Le Clair 1992). *A. maculatum* can live up to 28 years of age, as determined by skeletochronology, a technique used for aging amphibians (Flageole and LeClair 1992). During the post-breeding migration adults move away from the aquatic resource and into a summer foraging and eventually overwintering forested resource. Emigration and dispersal of both adults and juveniles is another phase of the life history of this species which requires movement through the landscape.

This research was conducted across a variety of habitats from primarily forested to heavily agricultural, within an overall landscape that is predominantly agricultural. Through a suite of analyses on these population level responses at multiple spatial scales I examine the effects of landscape structure on movement. I used a modeling approach, which enables an exploratory data analysis to be conducted where explicit hypotheses are not tested, but patterns in the data can be explored and the effects of multiple terms can be examined (McCullagh and Nelder 1989). This type of approach to the analysis of survey data enables further and more specific questions to be derived (Nicholls 1989). From these analyses I infer connectivity of the landscape and infer persistence for populations at small and broad spatial scales. Experimentally I examine the rate of movement of juvenile *A. maculatum* in forest and field habitats. I also develop a technique that will enable more information on the movements of juveniles to be obtained.

Chapter 1. The effects of landscape structure on the incidence and density of *Ambystoma maculatum* at local breeding sites.

Introduction

Unaltered landscapes are inherently heterogeneous (Turner *et al.* 1989; Fahrig and Merriam 1985; Taylor and Merriam 1996) and, by definition, usually provide adequate distribution of suitable habitat for local species. However, anthropogenic activities, such as agriculture, forestry and urbanization, result in changes to landscape structure that alter the inherent spatial heterogeneity through processes such as habitat destruction, fragmentation, and isolation (deMaynadier and Hunter 1995; Taylor and Merriam 1996).

For many organisms these changes can result in an increase in the amount of non-useable habitat throughout the landscape (Fahrig and Merriam 1985) and can contribute to the formation of small, isolated populations (Kareiva 1990). Movement between these heterogeneously distributed resources is critical for the persistence of populations (Fahrig and Merriam 1994). In addition, the rate of local extinctions is decreased by movement that enables access to required resources and movement between local populations, which contributes to "rescue" effects (Merriam 1991). The density of individuals in a population is usually negatively related to habitat loss (Andrén 1996), with a decrease in the number of individuals of a local population coinciding with an increase in the probability of extinction (Andrén 1994). It is the process of movement that mediates the effects of changes in landscape structure on the persistence of populations (Wiens 1995 and 1997).

Local populations of amphibians may be particularly susceptible to changes in landscape structure because most amphibians must move through the landscape between resources because of a biphasic life cycle (Wyman 1990; Blaustein *et al.* 1994; Gilhen 1984). As well, their terrestrial movements are physiologically constrained because of a need for aquatic and/or moist habitats (deMaynadier and Hunter 1998; Wyman 1990; Blaustein *et al.* 1994).

Research on amphibians indicates that an increase in habitat fragmentation and isolation can lead to an increase in the rate of local extinctions (Sjögren 1991; Gill 1978). In order to assess the effects of changes in landscape structure on the extinction of local populations the spatial extent of terrestrial habitat required must be known (Semlitsch 1998a). Semlitsch (1998a) quantified the spatial extent of terrestrial habitat required, for several amphibian species, by determining the maximum post-breeding movement distance. This distance was used as a means to delineate the extent to which a terrestrial buffer zone must be conserved around a wetland to ensure that the rate of local extinction does not increase.

The spatial extent of local populations of amphibians will depend primarily on the distribution of resources and the movement abilities of the organism (Hecnar and M'Closkey 1997). It is important to consider the types and amounts of habitats within the area surrounding their breeding site (Semlitsch 1998a). It is possible that there is a critical amount of habitat, a threshold amount, below which a local population could not persist (see Gibbs 1998a).

Yellow spotted salamanders, *Ambystoma maculatum* (Class: Amphibia) exhibit typical amphibian characteristics, which make them particularly susceptible to changes in landscape structure. Movement through the landscape is essential with an annual breeding migration from primarily moist, forested over-wintering and foraging sites to an aquatic breeding site (Gilhen 1984; Baldauf 1952; Whiteford and Vinegar 1966; Sexton *et al.* 1990; Semlitsch 1983). Aquatic breeding sites include temporary ponds, pools, puddles as well as permanent ponds and wetlands (Gilhen 1984; Freda *et al.* 1991; Woodward 1982). Breeding congregations of this species can be used to delineate a local population and their breeding migration offers an excellent opportunity for sampling adult populations. This allows the collection of data on incidence and density that reflects the movement ability of *A. maculatum*, and provides insight into the persistence of local populations (Kareiva 1990).

Forest is known to be the required terrestrial habitat of *A. maculatum* (deMaynadier and Hunter 1998) and yellow-spotted salamanders are known to be sensitive to forestry practices (deMaynadier and Hunter 1998) and other changes to the landscape such as human developments, including roads (Gibbs 1998b). The spatial extent of the landscape affects on populations is linked to the movement capabilities of *A. maculatum*. This species can move on average 150 m away from the pond during post-breeding migration (Douglas and Monroe 1981; Madison 1997). In experiments where individuals have been displaced away from a pond during their breeding migration it has been shown that they are capable of moving up to 500 m through the landscape (Shoop 1974). The maximum post-breeding migration movement tracked, however, was 220 m (Madison 1997). Few studies have explicitly examined the effects of landscape structure on population level responses, such as incidence and density, or on local population persistence. Those that have (see Gibbs 1998a) looked only broadly at these aspects of landscape structure and population responses. It is also known that within-pond characteristics are important in determining the persistence of populations of *A.*

maculatum and therefore the inclusion of a measure of within-pond variability may enable the elucidation of landscape effects.

To understand the effects of landscape structure on local populations of *A. maculatum*, and the spatial extent, I examined the influence of the proportion of forest on movement. This work was conducted in a highly altered landscape, at multiple spatial scales which incorporated distance classes, from the breeding pond out to 400 m for the analysis of incidence and 800 m for the analysis of the density of individuals migrating. Movement was examined by determining how the amount of forest around ponds influences incidence and density of *A. maculatum* at breeding ponds.

I addressed the questions: 1) Does the proportion of forest influence the incidence of *A. maculatum* at ponds and/or the density of *A. maculatum* caught at fences during their movement into ponds? 2) If there is an effect of landscape structure; at what spatial scales does it occur? 3) Do adults leave ponds in a random direction, or is their movement directed towards forested or field habitat?

Methods

Study Area

Surveys were conducted within the Annapolis Valley region of Nova Scotia, Canada (45°05'N; 64°30'W) (Appendix 1). The Annapolis Valley is a heterogeneous, predominantly agricultural landscape consisting of a mosaic of agricultural fields, including pastures and crop fields, as well as orchards, with forest distributed throughout. Ponds within this landscape are situated in both forested and agricultural habitats. The sixteen ponds selected (Appendix 2) for this survey of yellow-spotted salamanders

(*Ambystoma maculatum*) were all permanent ponds, constructed for agricultural irrigation. They ranged in age from 10 to 30 years, and varied in size from 80 m to 540 m in size. These ponds were selected in non-forested and forested habitats, with the proportion of forest surrounding the pond varying from 0-100%. Ponds were a minimum of 200 m apart and a maximum of 1.5 km apart. Selection of the ponds was based partially on accessibility and landowner permission.

Field Methods

Surveys of *A. maculatum* were conducted at the 16 ponds during the breeding migration, 29 April - 20 June 1997 (53 days). Migrating *A. maculatum* were intercepted at partial drift fences as they moved into and out of the breeding ponds. Fences consisted of a rigid synthetic material (donated by Weavex, Kentville, Nova Scotia) with side-flap pail traps (Nadorozny and Barr 1997) at each end and on both sides. Fences ranged in length from 20 m to 40 m and were placed between 10 m and 40 m from the pond edge. A total of 32 fences and 128 traps were constructed, with a pond having up to four fences. Fences were placed in forested and/or field habitats. Standardization of the length of fences, number, and location at the ponds was not possible due to topography.

All traps were checked daily and snout-vent length (SVL) and tail length were measured and recorded for all *A. maculatum* trapped. Individuals were sexed, with males being identified by the presence of a swollen cloaca and females recognized by a swollen (gravid) body (Gilhen 1984). Those individuals trapped on the side of the fence entering the pond were released into the pond and those trapped departing were released on the side of the fence away from the pond.

At each of the sixteen ponds I recorded the presence or absence of flow-through streams, and the presence or absence of red-spotted newts (*Notophthalmus viridescens).* *N. viridescens* were sampled at each pond between 7 May - 20 June 1997 using up to three aquatic, mesh, collapsible minnow traps, depending on the size of the pond.

Spatial scales were defined, with each scale containing different distance classes, measured in meters from the pond or fence. For the examination of the effects of landscape structure on the incidence of *A. maculatum* the small scale was defined as the area within a 200 m radius circle, including perimeter, and 100 m and 200 m from the pond as distance classes. The medium scale was defined as the circular area from the pond out to 400 m (Figure 1-1). At the perimeter I calculated the proportion of fence that was forested. At all other distance classes landscape structure was quantified as the proportion of forested habitat, including both coniferous and deciduous forest. The proportion of forest was calculated by placing a 2.5 mm^2 circular grid transparency centered over the pond on a 1:10 000 aerial photographs (1992) and determining the proportion of the total number of squares within the distance class that contained forest.

Within this analysis the greatest spatial extent examined did not extend beyond the 400 m distance class because the minimum distance between ponds was 200 m. At the 400 m distance class there was some overlap (maximum of 30% of the grid), but ponds were none-the-less treated as independent sampling points. This 400 m distance class is within the movement range of breeding individuals, where the average post-breeding migration is 150 m (Douglas and Monroe 1981) and the maximum recorded movement ability (after being displaced during the migration movement) is 500 m (Shoop 1974).

The analysis of density of individuals moving into ponds was conducted on the data from the ten ponds where *A. maculatum* was present. Density of individuals moving into the pond was quantified as the number of individuals trapped arriving per meter of fencing, for each of the 22 fences surrounding ponds where *A. maculatum* was present. For the analysis of density the small spatial scale was defined as the area within 200 m of the fence, with distance classes of 100 m and 200 m. The medium spatial scale was defined within the 400 m distance class and the broad scale included the area out to 800 m, containing the distance classes of 600 m and 800 m. For each distance class, landscape structure was measured as the proportion of forest within a 45 degree angle wedge which extended from the center of each of the 22 fences (Figure 1-2). A 2.5 mm^2 transparency grid was cut into a 45 degree angle wedge and was positioned over 1:10 000 aerial photographs (1992) and the proportion of the squares within the wedge that contained forested habitat was determined.

For this analysis the broad spatial scale encompassed a distance of 800 meters from the pond. This extent which is greater than that of the analysis of incidence, was possible because of the location of the partial drift fences and the nature of the wedge area analyzed. There was some overlap of forest at the 800 m distance class, (maximum of 30% of the grid), however, the fences were none-the-less treated as independent sampling points.

Statistical Analyses

The effects of the presence/absence of streams, red-spotted newts (*Notophthalmus viridescens)* on incidence of *A. maculatum* were examined through logistic regression analysis. The most significant variable was maintained and incorporated as a within-pond measure in the following analysis of incidence.

To examine incidence at the 16 ponds, four logistic regression models were constructed, one for each distance class, with the binary response variable presence or absence of *A. maculatum* at a pond. The term for the presence or absence of *N. viridescens* was always fit prior to the proportion of forest. To examine the density of *A. maculatum* at the 22 fences, five linear regression models were constructed, one for each distance class with a response variable of the log transformation of density. A term for pond was always fit prior to the proportion of forest term to account for variation in the number of individuals trapped across ponds. The model for the distance class where the proportion of forest term resulted in the greatest decrease in overall deviance was selected as the best model. Additional proportion of forest terms were added to determine if there were effects of the proportion of forest over and above that which appeared to be the most important (i.e. best model). Linear regression models were constructed to determine if there were effects of the direction of movement (arriving or leaving), or the habitat type (forest or field) in which the drift fence was placed, on the log transformed density of the total number of *A. maculatum* arriving and leaving at fences. To determine if adult arrival and departure from the pond was via the same habitat, an interaction of direction and fence habitat type were included in the linear regression model.

All models were constructed using S-plus statistics package (StatSci 1995) with a type I error rate of 5 percent. Each model was assessed visually using graphical residual diagnostics (McCullagh and Nelder 1989).

Results

Yellow-spotted salamanders (*Ambystoma maculatum*) were present at 10 of the 16 ponds sampled. Logistic regression analysis of the within-pond characteristics revealed there was a significant positive effect of the presence or absence *Notophthalmus viridescens* on incidence (Tables 1-1 and 1-2). There were no significant effects of the presence or absence of streams.

At the perimeter and 100 m distance classes, there was a significant effect of the proportion of forest on incidence over and above effects of the presence or absence of *N. viridescens* (Table 1-1). There were no significant effects of the proportion of forest at the 200 m distance class or the medium spatial scale (400 m) (Table 1-2). At the perimeter distance class, the logistic regression model was a poor fit and thus incidence is best modeled by the effects within the 100 m distance class (Table 1-1). The best model with the proportion of forest describing incidence was at the 100 m distance class. I detected no significant effects of the proportion of forest over and above the effects at the 100 m distance class. Within 100 m of the pond, as the proportion of forest increased, there was an increased probability that *A. maculatum* was present. *A. maculatum* was absent from ponds with less than 15% forest within 100 m, with one exception where the proportion of forest was greater than 50% (Figure 1-3) and *A. maculatum* was present.

There was a significant positive effect of the pond term within the linear models examining density (Tables 1-3, 1-4, and 1-5), indicating simply that the density of *A. maculatum* migrating through the landscape varied across ponds. At the small scale (100 m and 200 m) (Table 1-3) and the medium scale (400 m) (Table 1-4), there were significant positive effects of the proportion of forest within the wedge area extending from the fence. However, I detected no significant effects of the proportion of forest on density at the broad spatial scale (600 m and 800 m) (Table 1-5). For density, as with incidence, the best model was at the 100 m distance class (Table 1-3) and there were no multiple scale effects. This means that there were no effects of the proportion of forest on the log density of *A. maculatum*, over and above the effects of the proportion of forest within 100 m. Figure 1-4 shows that there is an increase in the log of density of *A. maculatum* per meter of fencing with an increase in the proportion of forest. The greater the amount of forest within 100 m of a fence, the greater the log density of *A. maculatum* at the fence.

Finally, there were significantly more individuals intercepted arriving at ponds than leaving (Table 1-6) and more individuals arrived and left at fences in forests than in fields (Figure 1-5). There was no significant interaction between direction and habitat type (Table 1-6), indicating that adults are arriving and leaving in the same direction (i.e. non-randomly).

Discussion

The amount of forest around breeding ponds influences the incidence and density of local populations of *A. maculatum* indicating that breeding migration movement is affected by landscape structure. Significantly more individuals were caught moving into breeding ponds through forest than fields, and there was a significant positive effect of the proportion of forest within 100 m of a pond on both incidence and density. This distance may represent the spatial extent of the terrestrial habitat because no effects of forest were detected over and above this.

The detection of landscape effects at this 100 m distance class corresponds well with the known post-breeding migration movement distances of *A. maculatum* which is, on average of 150 m (Kleeberger and Werner 1983; Douglas and Monroe 1981; Madison 1997). Semlitsch (1998a) determined that the spatial extent of the terrestrial habitat for pond breeding amphibians, including *A. maculatum*, was 164 m. This distance represents an upper limit of the average post-breeding movements for these species and was used for conservation purposes to delineate the required terrestrial buffer around wetlands (Semlitsch 1998). Semlitsch (1998a and b) recognized, however, that this approach was insufficient for assessing persistence because it did not assess the importance of the habitat between local populations.

There are several possible explanations for the detection of an effect of the proportion of forest at only the small spatial scale. Sexton *et al.* (1986) and Phillips and Sexton (1989) suggest that if resources are available in proximity to a pond and because there is a high level of competition for mates during the spring breeding season, it would be a reproductive disadvantage to move further than the average distance of 150 m away from the pond. Based on observations, Madison (1997) concluded that predation risk might influence shorter average post-breeding movement distances.

Although no effects of forest were detected beyond the small scale, the proportion of forest at a distance beyond 200 m may be important. It is possible that because of a small sample size (and thus a lack of statistical power) I was unable to detect any larger scale effects of the proportion of forest. To further examine possible broader scale effects a large-scale survey was conducted and the results are presented in Chapter 2.

My results of the analysis of incidence correspond with the results of a simulation modeling analysis by Venier and Fahrig (1996) in which they detected a significant positive relationship between the amount of suitable habitat and the distribution of a species (comparable to incidence). The detection of a significant landscape effect corresponds with results of other research which shows a positive relationship between incidence and the total amount of habitat for several amphibian species (see Vos and Chardon 1998, moor frogs (*Rana arvalis*); Sjögren 1991 and Sjögren-Gulve 1998, pool frogs (*Rana lessonae*); Loman 1981, common frogs (*Rana temporaria*); Vos and Chardon 1997, tree frogs (*Hyla arborea*)).

Venier and Fahrig (1996) also demonstrated, through simulation modeling, that there is a positive correlation between the amount of useable habitat and the density of individuals of a population. My results illustrate a significant positive relationship between the density of individuals migrating and the amount of useable forest habitat. Amphibian research has indicated that a decrease in density and local extinctions are related (Sjögren 1991; Laan and Verboon 1990; Reh and Seitz 1990) and can, in turn, influence the persistence of a local population (Sjögren 1991).

Andrén (1996), through simulation modeling, showed that there was a decrease in the proportion of occupied sites, for some species, when the proportion of required habitat decreased below 15 %. *A. maculatum* were absent from ponds that had less than 15 % forest within 100 m. This suggests that a threshold of forest habitat may exist, below which *A. maculatum* populations cannot persist. This concurs with the results of

Gibbs (1998a) who also suggested a threshold of proportion of forest for *A. maculatum*, however, he determined that populations were absent where forest was less than 30 %.

Results from the analysis of the density of *A. maculatum*, graphically (Figure 1-4) appears to show a threshold amount of forest at 30 %. The detection of a threshold for density of moving individuals coincides with my analysis of incidence and a threshold of 30 % forest coincides with the threshold detected by Gibbs (1998a). However, with a small sample size, and a limit in the range of possible habitat configurations, further surveys would have to be conducted to confirm this observation.

Andrén (1994) suggests that below this threshold amount of habitat, patch size and isolation factors (i.e. configuration) become important. Connectivity of the landscape is a function of both composition and configuration, however, it is not until the total amount of habitat drops below a threshold that the spatial arrangement, the configuration of the landscape, becomes important because of its effects on movement (Andrén 1994).

One pond was an exception; there was greater than 50% forest within 100 m, however, *A. maculatum* was absent. It is possible that the age of the pond could play a role in determining incidence. Laan and Verboom (1990), in studying the effects of population size and isolation on amphibian communities, determined that for new ponds age of the pond was the best predictor of incidence. The pond in the case described above was the youngest of all sixteen ponds (determined to be less than 10 years old according to local landowners) and it is possible that this pond has not yet been colonized by *A. maculatum*.

It is possible that there were other within-pond variables that affected incidence but were not measured in this survey. Other within-pond characteristics that could affect incidence of local populations include: size of pond, water quality, acidity, and agricultural pesticides and chemicals (Hecnar 1995). Including some of these may have enabled further insight into the direct effects of differences in landscape structure on movement by accounting for a greater portion of the variation in incidence.

All models of incidence did include the within-pond term presence or absence of red-spotted newts (*N. viridescens*). It is known that red-spotted newts prey on *A. maculatum* eggs and larvae (Gill 1978), however, I detected a significant positive effect of red-spotted newts on incidence. Gill (1978) similarly detected a non-negative effect of a predator species on a population of red-spotted newts. It is possible that the presence of red-spotted newts is providing an indication of the quality of the pond for amphibian occupancy in general. Thus if red-spotted newts were present there was a greater probability of *A. maculatum* being present.

To this point, I have explored movement indirectly through incidence and density. Another important aspect of the movement of adult *A. maculatum* is the orientation of arrival and departure movements at the breeding site. My results show that *A. maculatum* is arriving and leaving ponds through the same habitat, non-randomly, or targeted towards forest. This concurs with other research on *A. maculatum* which has indicated that individuals entered and exited a pond at the same location from one year to the next (Stenhouse 1985; Shoop 1965). Kleeberger and Werner (1983) showed that *A. maculatum* moved from breeding ponds in a direction towards adjacent marshland, where they spent the post-breeding season. My results show a significant orientation of movement toward forest, which is their post-breeding habitat and which concurs with Kleeberger and Werner (1983)

Several other amphibian species exhibit these non-random, or target-oriented movements, including the adult leopard frog (*Rana pipiens*) (Dole 1971), pool frog (*Rana lessonae*) (Sjögren-Gulve 1998b), striped newts (*Notophthalmus perstriatus*), eastern narrow-mouthed toads (*Gastrophryne carolinensis*) (Dodd and Cade 1998), and the juveniles of some of these species (Sjögren-Gulve 1998b). These non-random movements away from the breeding resources can have important implications for the dynamics and the persistence of spatially structured populations (Sjögren-Gulve 1998a).

This study demonstrates that the amount of forest within 100 m of a pond influences the movement of *A. maculatum* and thus the persistence of local populations. There appears to be a threshold amount of forest habitat below which local populations are not able to persist and that the smaller the proportion of forested habitat the smaller the density. Although these results indicate the importance of landscape features, such as forest, on local persistence, most amphibian populations do not function solely as isolated populations but as a system of interrelated populations (see Gill 1978; Sjögren 1991; Laan and Verboom 1990; Vos and Chardon 1997; Sinsch and Seidel 1995). Connectivity of the landscape between local populations is critical in structuring the dynamics of multiple populations. The spatial structure of populations of *A. maculatum* will be examined in the following chapter.

Table 1-1. Analysis of deviance table. Logistic regression model with the response variable incidence of *Ambystoma maculatum* at the small spatial scale, distance classes perimeter, 100 m and 200 m.

		Perimeter Distance Class			100 Meter Distance Class			200 Meter Distance Class		
Term	df	β	Dev	Pr(χ^2)	β	Dev	Pr(χ^2)	β	Dev	Pr(χ^2)
NULL	15		21.17			21.17			21.17	
Newts	1	3.27	5.73	0.017	2.74	5.73	0.017	2.34	5.73	0.017
Prop. Forest	1	7.29	7.62	0.006	5.50	3.89	0.049	3.91	1.96	0.161
Residuals	13		7.81			11.55			13.74	

Table 1-2. Analysis of deviance table. Logistic regression model with the response variable incidence of *Ambystoma maculatum* at the medium spatial scale, distance classes 400 m.

Term	df	β	Dev	Pr(χ^2)
NULL	15		21.17	
Newts	1	2.25	5.73	0.017
Prop. Forest	1	7.79	2.85	0.091
Residuals	13		12.58	

Table 1-3. Analysis of variance table. The response variable is the log transformed density of ***Ambystoma maculatum*** arriving per meter of fencing, at the small spatial scale, distance classes 100 m and 200 m.

		100 Meter Distance Class			200 Meter Distance Class		
Term	df	Mean Square	F	Pr(F)	Mean Square	F	Pr(F)
Pond	9	3.89	8.59	<0.001	3.89	5.32	0.006
Prop. Forest	1	11.63	25.70	<0.001	8.58	11.73	0.006
Residuals	11	0.45			0.73		

Table 1-4. Analysis of variance table. The response variable is the log transformed density of ***Ambystoma maculatum*** arriving per meter of fencing, at the medium spatial scale, distance class 400 m.

Term	df	Mean Square	F	Pr(F)
Pond	9	3.89	3.56	0.025
Direction	1	4.62	4.24	0.064
Residual	21	1.09		

Table 1-5. Analysis of variance table. The response variable is the log transformed density of ***Ambystoma maculatum*** arriving per meter of fencing, at the broad spatial scale, distance classes 600 m and 800 m.

		600 Meter Distance Class			800 Meter Distance Class		
Term	df	Mean Square	F	Pr(F)	Mean Square	F	Pr(F)
Pond	9	3.89	3.36	0.031	3.89	2.86	0.052
Prop. Forest	1	3.90	3.37	0.094	1.64	1.21	0.296
Residuals	11	1.15			1.36		

Table 1-6. Analysis of variance table. The response variable is the log transformed density of *Ambystoma maculatum*, number per meter of fencing, trapped arriving and departing.

Term	df	Mean Square	F	Pr(F)
Pond	9	6.08	6.82	<0.001
Direction	1	11.26	12.64	0.002
Habitat Type	1	6.54	7.34	0.013
Dir x Hab.Typ.	1	0.10	0.11	0.74
Residual	21	0.89		

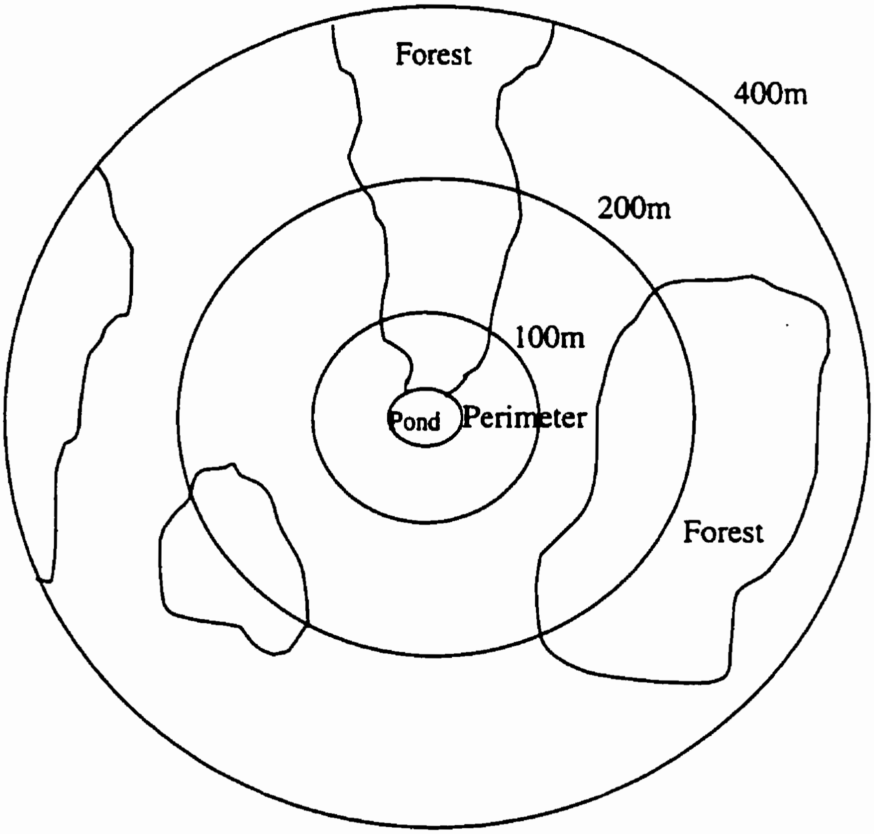

Figure 1-1. Schematic diagram depicting the configuration of the concentric circles and the distance classes used in the analysis of the incidence of *Ambystoma maculatum* at ponds (Diagram not to scale). Small scale: perimeter, 100 m, and 200 m distance classes, medium scale: 400 m distance class.

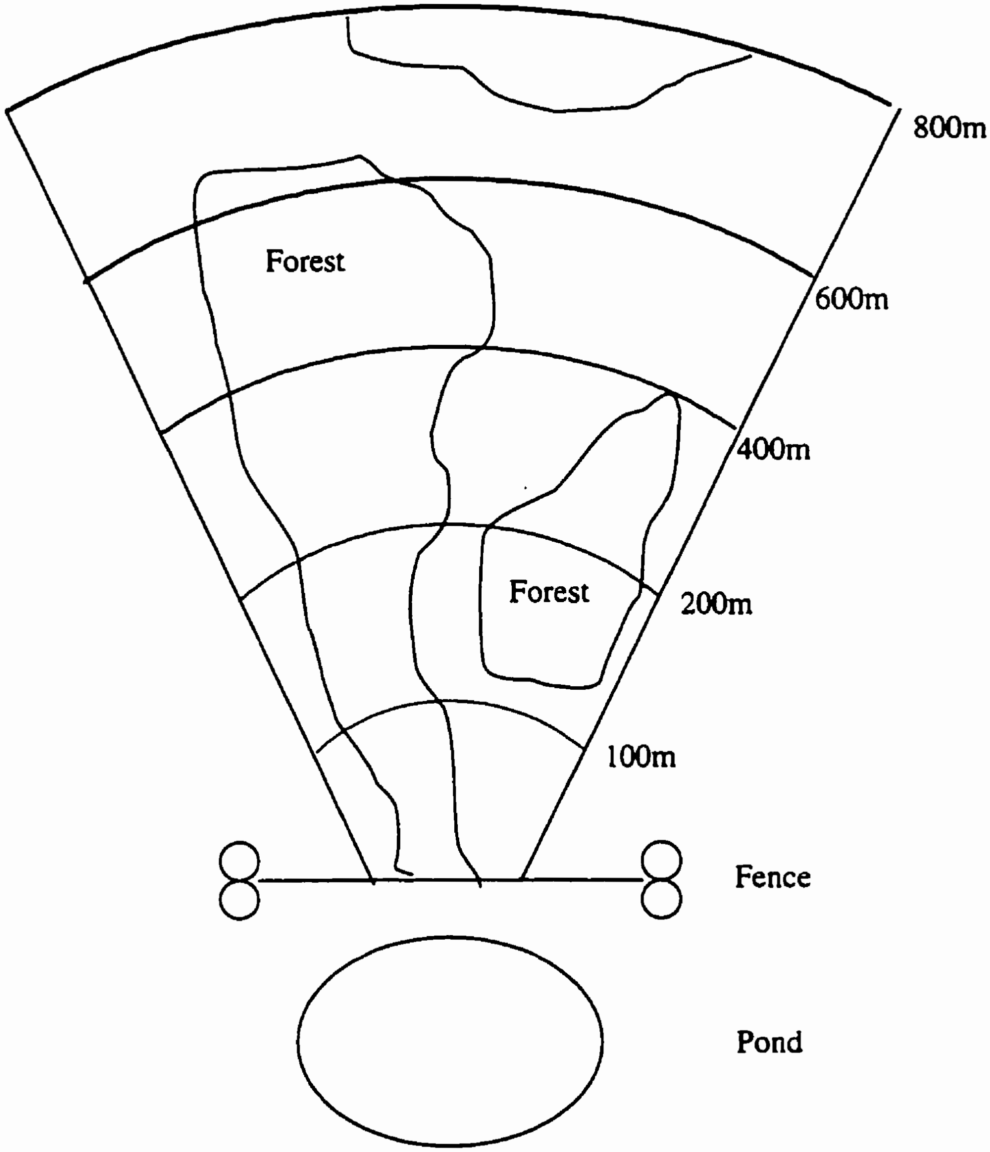

Figure 1-2. Schematic diagram depicting the configuration of the wedge and the distance classes used in the analysis of the log of the density of *Ambystoma maculatum* caught arriving at a fence (Diagram not to scale). Small scale: 100 m and 200 m distance classes, medium scale: 400 m distance class, broad scale: 600 m and 800 m distance classes.

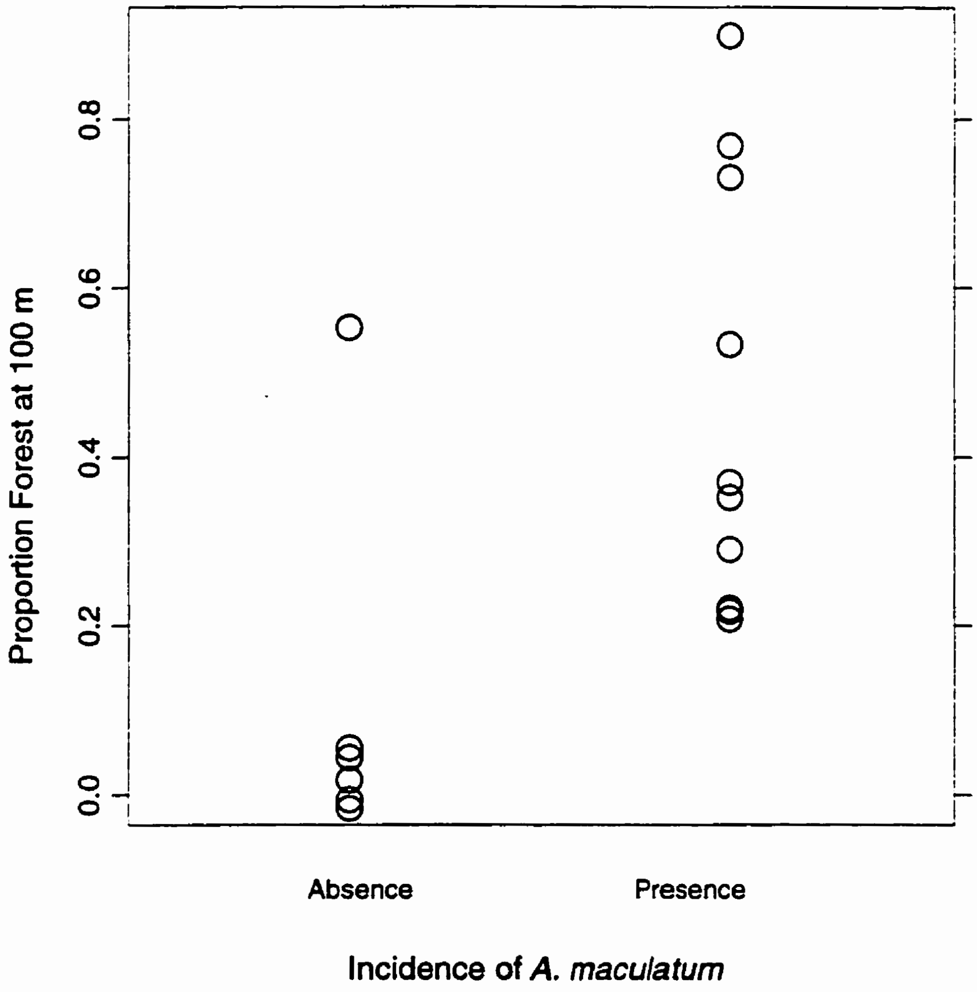

Figure 1-3. Relationship between the proportion of forest 100 m from a pond and the incidence of *Ambystoma maculatum*. Each dot represents a pond.

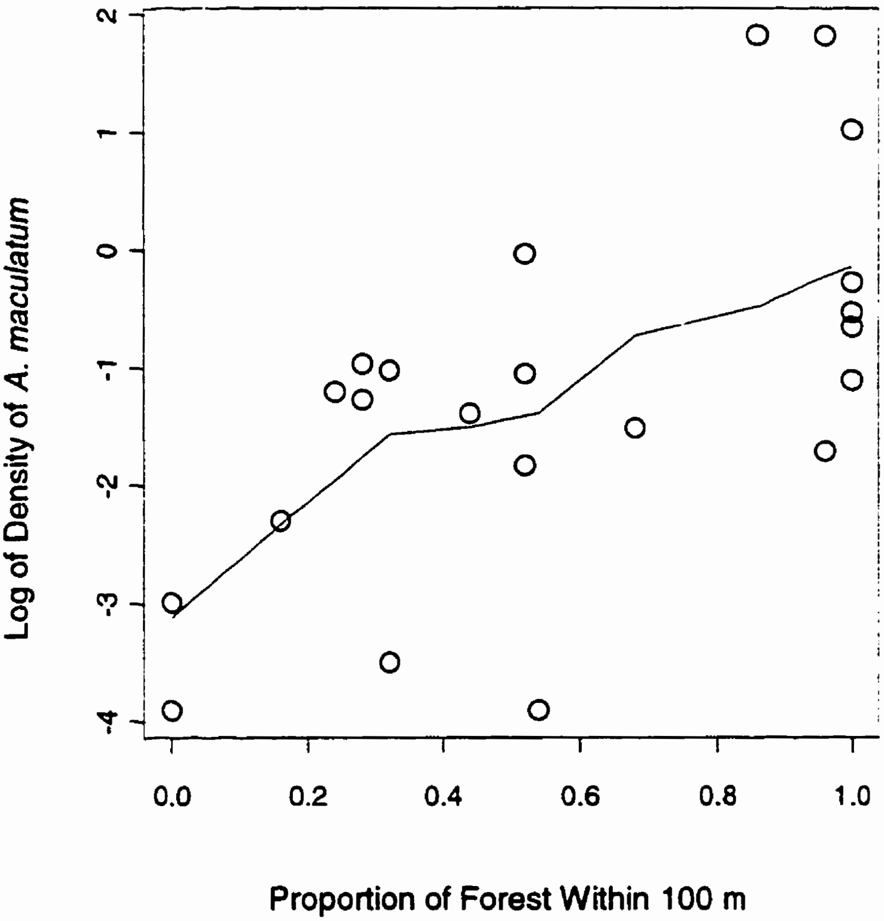

Figure 1-4. Significant positive relationship between the proportion of forest within 100 m of a pond and the log of the density of *Ambystoma maculatum* at a fence. Each dot represents a fence. Locally weighted regression line fit to the data.

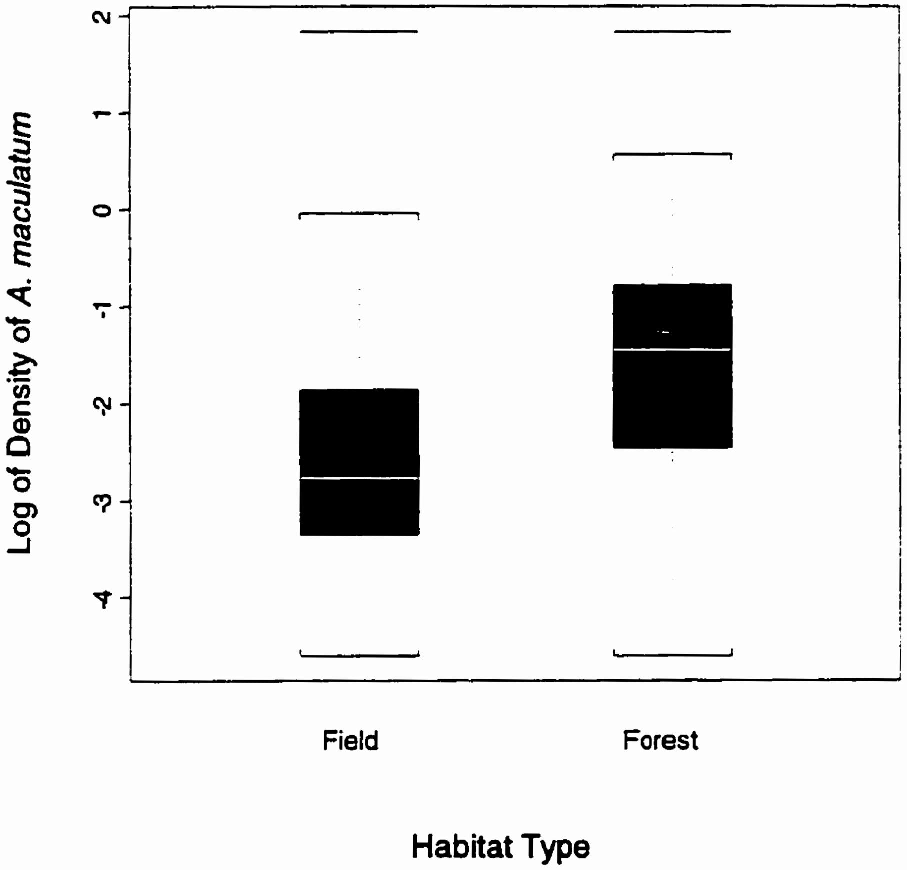

Figure 1-5. Box plot showing median (white line), interquartile range (box), range (whiskers), and outliers (bars) of the log of the density of *Ambystoma maculatum* caught at forest and field fences.

Chapter 2. The effects of landscape structure on the incidence and abundance of *Ambystoma maculatum* at multiple spatial scales.

Introduction

Populations can be susceptible to local extinctions due to resource quality, or changes in landscape structure that affect immediate movements (as demonstrated in Chapter 1). Persistence can also be affected by the spatial distribution of other populations because often these local populations are not isolated, but are part of a network. This network of local populations is termed a spatially structured population (Merriam 1991). Some research describes this network of local populations as a metapopulation, which is a specifically defined and parameterized spatially structured population model (Wiens 1997; Hanski and Simberloff 1997). The persistence of a spatially structured population can often be determined by employing a multiple spatial scale approach to ecological research (Turner *et al.* 1989; O'Neill *et al.* 1989; Wiens 1989).

There is an increase in the understanding of the importance of the process of movement in spatially structuring populations (Taylor 1997). Movement is the process that "connects" smaller populations (Kareiva 1990). The persistence of the overall multiple population structure is dependent upon the colonization, recolonization, emigration, and dispersal of individuals between populations (Baudry and Burel 1997). Dispersal is of particular importance in spatially structured populations (Johst and Brandl 1997; Sjögren-Gulve 1998b; Vos and Chardon 1998). Sjögren-Gulve (1998b) defines two types of dispersal, juvenile dispersal (movement from birth site to site of first breeding), and adult dispersal (movement of adults between successive breeding sites).

The dispersal pattern of organisms can be affected by changes in landscape structure including habitat loss, fragmentation, and increased isolation (Gibbs 1998a). The consequences of these changes to landscape structure, for populations, is an alteration of the connectivity of the landscape (Saunders *et al.* 1991; Vos and Chardon 1998).

Landscape connectivity is the degree to which the isolation of populations is prevented by the presence of landscape elements that allow organisms to move among resources (Merriam 1991). It was defined to help conceptualize how dispersal between resources mediates the interaction of landscape change on populations (Merriam 1991). The spatial extent of a network of populations must be determined and defined in any study because predictions of persistence varies according to spatial scale (Hecnar and M'Closkey 1997).

Many amphibian species do not form reproductively isolated populations, but instead a system of interacting local populations, a spatially structured population with sufficient movement and gene flow to enable persistence of the overall system (Sinsch and Seidel 1995; Reh and Seitz 1990). Some examples of amphibian species that show this spatial structuring of their populations include the red-spotted newt (*Notophathalmus viridescens*) (Gill 1978), moor frogs, (*Rana arvalis*) (Vos and Chardon 1998), and pool frogs (*Rana lessonae*) (Sjögren 1991) and are more specifically described within the context of a metapopulation model.

Local populations require specific resources that are distributed heterogeneously within the landscape. Thus individuals must move to access them (Merriam 1991). With increases in habitat loss and fragmentation, the distances and quality of the habitat between these required resources decrease (Fagrig and Merriam 1994). The consequences of these changes in landscape structure manifest themselves as an increase in the rate of local extinction and a decrease in the probability of persistence of the overall network of populations (see Sjögren 1991).

Some of the life history characteristics that make amphibians particularly susceptible to changes in the landscape are its required movements between aquatic and terrestrial habitat, philopatry, and limited dispersal capabilities (Wyman 1990; Blaustein *et al.* 1994). Strong site fidelity of adults reduce the probability of movement between resources (Wiens *et al.* 1993) and landscape changes can result in a decrease in connectivity and thus lower the rate of colonization and recolonization of local populations for some species (Weins 1995).

Again, dispersal is the process that mediates the effects of landscape change on multiple populations (Kareiva 1990). The limited dispersal capabilities of amphibians can have consequences for the persistence of a network of populations. Dispersal enables the colonization and recolonization of populations, as well as the "rescuing" of local populations near extinction (Gill 1978). The changes to the landscape that limit amphibian dispersal do so by decreasing the degree of connectivity of the landscape for a particular species (Marsh and Pearman 1997; Vos and Chardon 1998). Some landscape features, such as forest (Laan and Verboon 1990) and streams (Gibbs 1998b; Berman and Saproznikov 1994) may increase the connectivity of the landscape for some amphibians. Agricultural fields and roads have been identified as features in the landscape that decrease connectivity for some amphibian species (Mader 1984; Gibbs 1998b; deMaynadier and Hunter 1995; Vos and Chardon 1998; Reh and Seitz 1990). Research has indicated that the connectivity of the landscape is important in the persistence of spatially structured populations of amphibians (see Sjögren 1991; Sjögren-Gulve 1994; Laan and Verboon 1990; Vos and Chardon 1998).

In chapter 1, I showed that landscape features influence the movement and persistence of local populations of *A. maculatum.* In this study I examine the effects of landscape features on the incidence and abundance of *A. maculatum* of local populations of *A. maculatum* at multiple spatial scales to assess the population spatial structure. After accounting for any local effects I have indirectly to determined whether any other landscape features significantly affect the movement and thus persistence of *A. maculatum* populations.

Methods

Study Area

Surveys were conducted within the Annapolis Valley region of Nova Scotia, Canada (45°05'N; 64°30'W) (Appendix 1). The Annapolis Valley is a heterogeneous, predominantly agricultural landscape consisting of a mosaic of agricultural fields, including pastures and crop fields, as well as orchards with forest habitat and ponds distributed throughout. Most ponds within this area are constructed for agricultural irrigation, are permanent, and are fed either by natural spring or stream inflow. Others are natural ponds and some are ephemeral. The ponds range in age and size. Many of these ponds provide suitable breeding habitat for yellow-spotted salamanders (*Ambystoma maculatum*).

Field Methods

Within approximately a 40 x 20 km region of the Annapolis Valley more than 200 ponds were located visually by examining topographic maps, driving every road in the region, and talking to landowners. 56 ponds were selected (Apendix 3) from every other 1 x 1 km square on topographic maps (in a checkerboard pattern). Within each square the ponds selected were a minimum of 1.5 km apart, a distance greater than the known movement range of *A. maculatum*. Ponds selected were a maximum of 250 m in perimeter, which is a suitable pond size for breeding *A. maculatum*, however, ponds exceeding this size were not included due to the logistical limitations of searching larger ponds. The survey included ponds that were permanent or temporary and either constructed or natural. Ponds were surrounded by forest, agricultural habitat (including pasture, crop field, or orchard), landscaped lawn, or combination of these habitats. If an identified square from the topographic map had more than one pond meeting these criteria only one pond was selected at random. If a square had no ponds with these criteria then the next nearest square in which there was a pond that met the criteria was selected.

The survey was conducted at 56 ponds from 2 May - 12 May 1998. The survey was initiated after *A. maculatum* egg masses were observed at a known breeding site, ensuring that the breeding season had started. Sampling occurred within a ten day period to ensure survey was completed prior to the hatching of larvae. The occurrence of *A. maculatum* was sampled by conducting a survey of egg masses at each of the 56 ponds selected. *A. maculatum* egg masses are very distinct from the other amphibian species (the Ranidae) in this geographic area (Gilhen 1984). Two researchers conducted the sampling, one on shore and one wading at edge of the water parting all vegetation and carefully moving any surface debris. The search zone was approximately one meter wide and one meter deep and the entire perimeter of each pond was searched. Incidence was determined by observation of the presence or absence of egg masses. If no egg masses were observed on the first visit ponds were visited a second time. Brodman (1995) suggests that *A. maculatum* females can lay more than one egg mass with between 55-88 eggs, thus the total count of egg masses does not necessarily reflect the number of individuals at the pond. However, the total number of egg masses at a pond was used as a measure of relative abundance.

I measured the perimeter of each pond using a string box and in addition, observations of the presence or absence of stream inflows and outflows, and the relative slope of the pond (shallow and steep) were recorded. Females attach their egg masses to the base of emergent vegetation (Stangel 1988). This position can affect the success of development of the embryos (Broodman 1995). The presence or absence of emergent vegetation was therefore recorded and included any grass, sedge, cattail, alder, and willow branches, each of which provide material for the attachment of egg masses. At each pond the pH and the total dissolved solids (parts per million) were measured using hand held meters and the average of three samples was recorded. The presence or absence of red-spotted newts (*N. viridescens*) and fish were made based on visual observation. The presence or absence of the American toad (*Bufo americanus*) was recorded and the presence or absence of any *Rana* species, including (*Rana clamitans, Rana pipiens, Rana sylvatica, Rana catesbiana*) were recorded based on visual identification of adults, egg masses, by the presence of tadpoles, or by their mating calls. Spring peepers (*Hyla crucifer*) were recorded based on hearing mating calls.

The landscape structure surrounding each pond was measured from scanned 1:10 000 aerial photographs (1992) using an image analysis program. Analysis was conducted at three spatial scales, defined by different distance classes and which encompass the landscape within the areas of circles with radii of 100 m and 250 m (small scale), 500 m (medium scale), and 750 m and 1000 m (broad scale) from the center of the pond. The landscape structure variables recorded within each of these scales included the proportion of the area that was forested (including both deciduous and coniferous forests) and the total length of roads (not including any small, private, low traffic roads). The total length of road was standardized by recording it as the number of meters per 1000 m^2 area.

Statistical Analyses

Prior to any modeling analysis, a Mantel test was conducted to assess the presence of spatial autocorrelation in the response variables, incidence and abundance. If spatial autocorrelation was present, a linear spatial term (i.e. the easting and northing) and non-linear spatial term (i.e. the square of the easting and northing) were included in the models. To ensure that the inclusion of spatial terms in the models accounted for the spatial autocorrelation, a second Mantel test was conducted on the residuals of the model.

Logistic regression models were constructed to examine the effects of within-pond characteristics and the proportion of forest on the incidence of *A. maculatum* at each of the five distance classes. The within-pond variables and proportion of forest were fit in a stepwise fashion after any spatial terms, and the size of the pond. All non-significant within-pond terms (p-value < 0.05) were excluded form the model.

A highly significant negative correlation existed however, between the pH of ponds and the proportion of forest, with the strongest correlation at 250 m distance class. A linear regression model was therefore constructed at the 250 m distance class, with pH modeled by the proportion of forest. The residuals of the model represented the effects of pH on incidence over and above any small scale effects of the proportion of forest. These residuals were used as a new pH term in the logistic regression models of incidence.

Five separate logistic regression models were again constructed, one for each distance class, including spatial terms, perimeter, and the new pH term prior to the fitting of the proportion of forest term. All statistical models were fit using the generalized linear model (GLM) procedures (Chambers and Hastie 1993) in S-plus (StatSci 1995). Each model was assessed visually using graphical residual diagnostics and the significance of each term was tested against a χ^2-distribution (McCullagh and Nelder 1989).

The model for the proportion of forest term that resulted in the greatest decrease in overall deviance was selected as the best model. Additional effects of the proportion of forest, and the total length if road, at distance other than that which appeared to be the most important (i.e. best model) were examined to determine if there were additional landscape effects.

The analysis of abundance included only ponds at which *A. maculatum* egg masses were present (n = 32). This response variable, with count data, number of egg masses per pond, would typically follow a Poisson distribution, but our data was overdispersed (with the variance in the response increasing with the square of the mean). Therefore the most appropriate generalized linear model was that with the gamma distributed errors and the log link (Chambers and Hastie 1993; McCullagh and Nelder 1989). Generalized linear models with gamma distributed errors and a log link were used to assess the effects of within-pond characteristics and landscape variables on the abundance of egg masses at each pond.

In order to account for variability in the size of ponds sampled, the perimeter term was fitted first in all models and the effects of other within-pond variables and the effects of the proportion of forest were assessed over and above the effects of perimeter. Any significant within-pond terms were maintained in the model (p-value < 0.05). Five separate generalized linear models were constructed, one for each distance class, and the effects of the proportion forest was assessed for each. Models were assessed visually using residual diagnostics and the significance of each term was tested against a χ^2-distribution. As with the analysis of incidence the best model was selected and any effect of the proportion of forest or the total length of road at other distance classes, over and above the effects of proportion forest at the best scale, were examined.

Results

Ambystoma maculatum were present at 32 of the 56 ponds sampled. There were no significant effects of emergent vegetation, slope, presence or absence of predators or competitors or streams, or total dissolved solids on incidence or abundance. One pond with a very high total dissolved solids measurement was excluded from future analysis. Ponds with a pH greater than 8 or less than 6 had no *A. maculatum* (8 of 55 ponds)

(Figure 2-2). Of the ponds with pH between 6 and 8 ($n = 47$) results of a Mantel test for spatial autocorrelation of incidence were significant (average p-value = 0.015). Logistic regression analysis revealed a significant effect of the linear term, easting and the non-linear term, easting squared on the incidence of *A. maculatum* (Table 2-1, 2-2, and 2-3). This indicates that the spatial location of the ponds must be accounted for prior to examining the direct effects of landscape structure on incidence. In the second Mantel test of the residuals of this model of incidence, no additional significant spatial autocorrelation effects were detected (average p-value = 0.152). Thus the easting and easting squared terms were included in the models prior to fitting any other term, eliminating any effect of spatial autocorrelation.

The logistic regression analysis revealed that, over and above the effects of spatial location, the size of the pond has a significant effect on incidence (Table 2-1, 2-2, and 2-3). As the size of the pond increases, the probability that the pond would be occupied decreases (Figure 2-3). Also, the logistic regression analysis revealed that, over and above the effects of spatial location and size of the pond, the probability of *A. maculatum* being present at a pond decreased as the pH of the pond increased (Figure 2-4). pH however, was significantly negatively correlated with the proportion of forest; highest correlation at the 250 m distance class (Figure 2-5). Thus the residuals of this linear model were used as the new pH term in subsequent logistic regression models.

There was a negative relationship between the new pH term and incidence (Table 2-1, 2-2, and 2-3). Further, a significant positive effect of proportion of forest was detected at 500 m, 750 m, and 1000 m distance classes (Table 2-2 and 2-3). The best model of incidence included the proportion of forest at the broad spatial scale (1000 m distance class).

Figure 2-6 illustrates that with an increase in the amount of forest within 1000 m of the pond there is an increase in the probability that A. *maculatum* will be present. This provides indication that the connectivity of the landscape for A. *maculatum* is important at broad spatial scales.

The total length of roads at the small spatial scale (100 m and 250 m) had a significant negative effect on incidence when examined over and above the effects of the proportion of forest at 1000 m (Table 2-4). There were no significant effects of the total length of roads at medium or broad spatial scales.

No significant spatial autocorrelation was detected in the response variable, abundance (average p-value = 0.155). There was a significant positive effect of pond size on abundance (Table 2-5, 2-6, and 2-7; Figure 2-7), contrary to the effects of size of pond on incidence. There was a significant effect of the proportion of forest, fitted after the perimeter term, at each scale, except the 100 m distance class. The model explaining the greatest amount of variation included the proportion of forest at the 250 m distance class (Table 2-5). The greater the amount of forest within 250 m, the greater the number of A. *maculatum* egg masses, i.e. the greater the relative abundance (Figure 2-8).

There were no significant effects of the proportion of forest over and above the effects in this best model (Table 2-3 and 2-4). This indicates that there are no multiple scale effects of landscape structure on abundance. As with incidence, the total length of roads had a significant negative effect on abundance at the small spatial scale (100 m and 250 m) when examined over and above the effects of the proportion of forest at 250 m

(Table 2-8). There were no significant effects of the total length of roads on at medium or broad spatial scales.

Discussion

I determined that populations of yellow-spotted salamanders (*Ambystoma maculatum*) are spatially structured. After accounting for within-pond variation, incidence of *A. maculatum* egg masses was significantly affected by the proportion of forest at 1000 m. Abundance was significantly affected by the proportion of forest at 250 m and both incidence and abundance by the total length of road within 250 m. The examination of these landscape effects is important in determining the spatial structure of *A. maculatum* populations and their persistence.

Examining the effects of changes in landscape structure on local scale movements, in Chapter 1, I determined that local population persistence was influenced by immediate landscape features, i.e. proportion of forest within 100 m. It is known that adult *A. maculatum* move on average 150 m during post-breeding migration (Shoop 1974). Therefore the detection of a landscape effect at 1000 m indicates that there is a process over and above adult movement being affected by landscape structure. The presence of spatial autocorrelation also provides indication that there is a broad scale spatial process influencing incidence. The presence of spatial autocorrelation indicates that samples are more similar at a specific distance than would be expected by chance alone (Legendre and Fortin 1989). The underlying process that is responsible for this can vary across spatial scales, but provides indication of a link between these samples at that distance class. The minimum distance between ponds sampled was, *a priori*, selected at

800 m because this was beyond the known adult movement range, therefore the presence of autocorrelation demonstrates that there is an underlying process structuring populations of *A. maculatum* which occurs beyond 800 m (the minimum distance compared in the spatial autocorrleation test). It is not unexpected that *A. maculatum* populations are spatially structured because there are a number of different amphibian species that exhibit spatial structuring (Sjögren 1991; Vos and Chardon 1998; Berman and Saproznikov 1994).

More specifically, dispersal movements "connect" populations within a spatially structured populations, or network of populations (Vos and Chardon 1998). Dispersal can be negatively or positively affected by landscape structure. In an agricultural landscape, small isolated habitat patches located within a matrix of inhospitable habitat (Laan and Verboom 1990) can make dispersal to suitable habitats very difficult. Vos and Chardon (1997) and Merriam (1991) determined that dispersal would be more successful in a landscape the larger proportion of suitable terrestrial habitat as a result of an increase in the connectivity of the landscape.

Other amphibian research has demonstrated this link between persistence, movement, landscape change, and connectivity of the landscape. Sjögren (1991) determined that connectivity was critical to the persistence of a metapopulation of pool frogs (*Rana lessonae*), where there was an increase in the probability of extinction with an increase in distance between populations. Laan and Verboon (1990) showed that the proximity of forest habitat is positively related to species number and interpreted this as forest increasing connectivity, thus improving access to required resources. In studying the moor frog (*Rana arvalis*), Vos and Chardon (1998) detected a significant positive effect of the proportion of suitable habitat (moorland) at small and broad scales. They regarded the proportion of suitable habitat over broad spatial scales as increasing the connectivity of the landscape, thus increasing the colonization probability of a pond within that landscape (Vos and Chardon 1998). My results also show a greater probability of occupancy of a breeding site as the proportion of forest increases suggesting an increase in connectivity of the landscape for *A. maculatum.*

As described in the introduction, there are two types of dispersal, juvenile and adult. Thus the effects of changes in landscape structure on connectivity and population persistence on both adult and juvenile movements should be considered. For many amphibian species it is recognized that dispersal is accomplished primarily during the juvenile phase (Breden 1987; Schroeder 1976; Dole 1971; Berman and Sapozhnikov 1997). There is little known about the movement abilities of juvenile *A. maculatum* (Shoop 1974) or the sub-adult stage, which can range from two to six years of age (Flageole and LeClaire 1992). For *A. maculatum* populations, more knowledge of the movements of juveniles and sub-adults is required before it can be definitively stated that the process of movements during these phases is the primary process responsible for the spatial structuring of these populations. Adult dispersal movements between breeding ponds can also play a role in the spatial structuring of the *A. maculatum* populations and their movements can be influenced by changes in the landscape.

In chapter 1, I detected a significant directed movement pattern of adults into and out of ponds, directed towards forest. This non-random dispersal maintains the traditional philopatric patterns of movement and thus decreases the probability of colonization or recolonization and therefore could have a negative implications for a multiple population (Sjögren-Gulve 1998). The consequences of non-random dispersal are primarily associated with juveniles, but adults may also fulfil a role in advancing the persistence of the spatially structured population by dispersing via shorter movements annually between ponds. For some amphibian species, Sjögren-Gulve (1998) describes how movements to an adjacent habitat may act as a "stepping stone" for the next years movement to a neighboring breeding pond. Although contrary to known philopatric behaviours of *A. maculatum*, some individuals breed in ephemeral bodies of water which vary in their existence year to year. Thus, even if these individuals return to a previous years ephemeral aquatic site, it may not exist and they would continue their movements in search of an available breeding site. Thus temporary breeding sites may act as "stepping stones" yearly, contributing to the exchange of adults between local populations and contributing to the overall multiple population persistence.

This contribution to the persistence of populations may, however, be minimal because *A. maculatum* exhibits a high breeding site fidelity (Whiteford and Vinegar 1966; Stenhouse 1985; Whiteford and Vinegar 1966). Philopatry is known to reduce the probability of movement between patches and in turn persistence of local populations (Wiens *et al.* 1993).

I have determined that forest is a feature of the landscape that enhanced connectivity for populations of *A. maculatum*, however there are other landscape features that could decrease connectivity. I determined that roads have a negative influence on incidence and abundance of adult *A. maculatum* at small spatial scales (100 m and 250 m). Roads can increase the rate of extinction by decreasing the amount of suitable habitat, decreasing the size of the local habitats, changing the biotic and abiotic properties of habitats, and by altering the arrangement and connectivity of habitats (Reh and Seitz 1990; Mader 1984). It is known that roads negatively influence the persistence of amphibian populations by increasing mortality (Fahrig *et al.* 1995), decreasing connectivity (Vos and Chardon 1998; Gibbs 1998b), and affecting the genetic composition by acting as barriers to the flow of genes (Reh and Seitz 1990).

I do not know if the negative effect of roads on the incidence and abundance of *A. maculatum* is through increases in mortality, or through a barrier effect to movement at the small scale which decreases the connectivity between required terrestrial habitat and the breeding site. Other research with *A. maculatum* has also detected significant negative effects of roads on incidence (Gibbs 1998b; deMaynadier and Hunter 1995) and on abundance (Vos and Chardon 1998). deMaynadier and Hunter (1995) determined that *A. maculatum* movement was inhibited by roads due to a decrease in the amount of habitat. Gibbs (1998b) however, could not distinguish between an effect of roads due to an increase in mortality or a decrease in connectivity. Vos and Chardon (1998) detected a negative effect of roads on the abundance of moor frogs (*Rana arvalis*) but were also unable to determine the cause of the decrease.

There was a significant positive effect of the proportion of forest on abundance at the small spatial scale (250 m). In a study of *Rana dalmatina*, using a similar sampling, i.e. counts of egg masses as a measure of relative abundance, Wederkinch (1988) detected landscape effects on abundance. He detected an almost exponential decrease in the number of egg masses with increasing distance from the nearest forest (Wederkinch 1988). No effects beyond the small scale were detected which concurs with Chapter 1 and with Vos and Chardons' (1998) multiple scale analysis where they found a positive effect of the proportion of moorland on the abundance of moor frogs (*Rana arvalis*).

The within-pond variable, pond size, had a significant positive effect on abundance. Vos and Chardon (1998) detected a significant positive effect of pond size on the probability of occurrence for moor frogs (*Rana arvalis*). It is possible that the larger the pond the greater the chance for an individual to intercept it. Laan and Verboom (1990) determined that the size of a pond was the best predictor of the number of species and it has been suggested that, for abundance, pond size is the limiting factor for some amphibian species (Vos and Chardon 1998). In situations where the landscape is fragmented, however, research, such as Loman's (1981) work with *Rana temporaria* and Vos and Chardon (1997) work with *Hyla arborea*, indicate that it is the distribution of suitable terrestrial habitat that will be the more limiting factor in abundance. This concurs with the significant effects of the proportion of forest that I have shown.

For the incidence of *A. maculatum*, pond size had a significant negative effect on the probability of the presence of *A. maculatum* at a pond, which is different than the effects of pond size on abundance. Sjögren (1991) also detected a negative effect of pond size for pool frogs (*Rana lessonae*) and suggested this could be explained by the occurrence of fish predation in larger ponds. However, I did not detect a significant effect of the presence or absence of fish on incidence so it is possible that there are other within-pond variables that influence incidence through the effects of pond size.

pH was important in determining the incidence of *A. maculatum* at breeding sites. *A. maculatum* were absent from ponds with a pH of less than 6 or greater than 8. This concurs with other research which has identified *A. maculatum* as a species sensitive to water acidity where pH levels between 4 and 5 increase egg mortality (Freda *et al.* 1991; Pough and Wilson 1977; Pierce 1985). With ponds over pH 8 and under pH 6 excluded, I detected a significant negative effect on incidence which suggests that a decrease in pH results in a greater probability of *A. maculatum* being absent from ponds.

Contrary to the results of Chapter 1, there was no direct effect of the proportion of forest on incidence at the small scale. This difference could be a function of the additional within-pond characteristics that were recorded and incorporated in this survey. These additional within-pond variables could have altered the detection of the small scale landscape variables due to the presence of a relationship between the two. I determined that there were indirect effects of the proportion of forest on incidence through a significant negative relationship between the proportion of forest at 250 m and pH. Although I cannot directly attribute causation for the relationship between the proportion of forest and pH, it is known that the composition of forest can affect the pH of surrounding soils and waters (Wyman 1988) and therefore be having an influence on the incidence of *A. maculatum* at ponds.

Vos and Chardon (1998) conducted a survey with a statistical analysis similar to this study and they too detected a high degree of correlation between within-pond and landscape variables when included in the same model. However, they simply excluded the within-pond term to enable analysis of the landscape variables (Vos and Chardon 1998). I modeled landscape effects after accounting for these correlated terms and therefore was able to examine the effects over and above small scale effects to determine that there were broad scale effects of the proportion of forest.

A. maculatum populations are spatially structured; they exist as a network of local populations where movement between resources at a small scale and between populations at a broad scale is critical for persistence. The amount of forest influences connectivity and persistence at a small scale and out to 1000 m. Further research is needed to confirm the role of dispersal movements in the spatial structuring of these populations.

Table 2-1. Analysis of deviance table. Logistic regression models with the response variable incidence of *Ambystoma maculatum*, at the small spatial scale, distance classes 100 m and 250 m.

		100 Meter Distance Class			250 Meter Distance Class		
Term	df	β	Dev	Pr(χ^2)	β	Dev	Pr(χ^2)
NULL	46		58.87			58.87	
Easting	1	+	3.66	0.056	+	3.66	0.056
Easting^2	1	-	3.77	0.052	-	3.77	0.052
Perimeter	1	-0.02	8.17	0.004	-0.02	8.17	0.004
New pH	1	-1.41	4.91	0.027	-1.48	4.91	0.027
Prop. Forest	1	1.52	0.523	0.470	2.06	2.06	0.151
Residuals	41		37.83			36.29	

Table 2-2. Analysis of deviance table. Logistic regression models with the response variable incidence of *Ambystoma maculatum* at the medium spatial scale, distance classes 500 m.

Term	df	β	Dev	Pr(χ^2)
NULL	46		58.87	
Easting	1	+	3.66	0.056
Easting^2	1	-	3.77	0.052
Perimeter	1	-0.02	8.17	0.004
New pH	1	-1.45	4.91	0.027
Prop. forest	1	3.22	2.68	0.102
Residual	41		35.67	

Table 2-3. Analysis of deviance table. Logistic regression models with the response variable incidence of *Ambystoma maculatum* at the broad spatial scale, distance classes 750 m and 1000 m.

		750 Meter Distance Class			1000 Meter Distance Class		
Term	df	β	Dev	Pr(χ^2)	β	Dev	Pr(χ^2)
NULL	46		58.87			58.87	
Easting	1	+	3.66	0.056	+	3.66	0.056
Easting^2	1	-	3.77	0.052	-	3.77	0.052
Perimeter	1	-0.02	8.17	0.004	-0.02	8.17	0.004
New pH	1	-1.41	4.91	0.027	-1.40	4.91	0.027
Prop. Forest	1	3.94	4.29	0.038	3.03	4.91	0.049
Residuals	41		34.07			33.44	

Table 2-4. Analysis of deviance table. Logistic regression models with the response variable incidence of *Ambystoma maculatum* including effect of total length of road at small spatial scales, distance classes 100 m and 250 m.

		100 Meter Distance Class			250 Meter Distance Class		
Term	df	β	Dev	$Pr(\chi^2)$	β	Dev	$Pr(\chi^2)$
NULL	46		58.87			58.87	
Easting	1	+	3.66	0.056	+	3.66	0.056
Easting^2	1	-	3.77	0.052	-	3.77	0.052
Perimeter	1	-0.02	8.17	0.004	-0.02	8.17	0.004
New pH	1	-1.15	4.91	0.027	-1.12	4.91	0.027
Prop. Forest (at 1000m)	1	4.98	4.91	0.027	3.20	4.91	0.027
Road	1	-16.6	5.56	0.018	-7.72	5.75	0.016
Residuals	41		27.88			27.69	

Table 2-5. Analysis of deviance table. Generalized linear model (with gamma errors and a log link). The response variable is the abundance of *Ambystoma maculatum* egg masses, for the small spatial scale, distance classes 100 m and 250 m.

		100 Meter Distance Class			250 Meter Distance Class		
Term	df	β	Dev	Pr(χ^2)	β	Dev	Pr(χ^2)
NULL	31		57.69			57.69	
Perimeter	1	0.01	11.50	<0.001	0.02	11.50	<0.001
Prop. Forest	1	0.28	0.09	0.768	2.66	7.83	0.005
Residuals	29		46.10			38.35	

Table 2-6. Analysis of deviance table. Generalized linear model (with gamma errors and a log link). The response variable is the abundance of *Ambystoma maculatum* egg masses, for the medium spatial scale, distance class 500 m.

Term	df	β	Dev	Pr(χ^2)
NULL	31		57.69	
Perimeter	1	0.02	11.50	<0.001
Prop. forest	1	2.55	7.64	0.006
Residual	29		38.54	

Table 2-7. Analysis of deviance table. Generalized linear model (with gamma errors and a log link). The response variable is the abundance of *Ambystoma maculatum* egg masses, for the broad spatial scale, distance classes 750 m and 1000 m.

		750 Meter Distance Class			1000 Meter Distance Class		
Term	df	β	Dev	Pr(χ^2)	β	Dev	Pr(χ^2)
NULL	31		57.69			57.69	
Perimeter	1	0.02	11.50	<0.001	0.02	11.50	<0.001
Prop. Forest	1	2.54	7.77	0.005	2.14	5.31	0.021
Residuals	29		38.00			40.88	

Table 2-8. Analysis of deviance table. Generalized linear model (with gamma errors and a log link). The response variable is the abundance of *Ambystoma maculatum* egg masses, including the effect of total length of road at the small spatial scale, distance class 100 m.

Term	df	β	Dev	$Pr(\chi^2)$
NULL	31		57.69	
Perimeter	1	0.02	11.50	<0.001
Prop. forest (at 250m)	1	3.26	7.83	0.005
Road	1	-4.89	4.69	0.030
Residual	29		33.67	

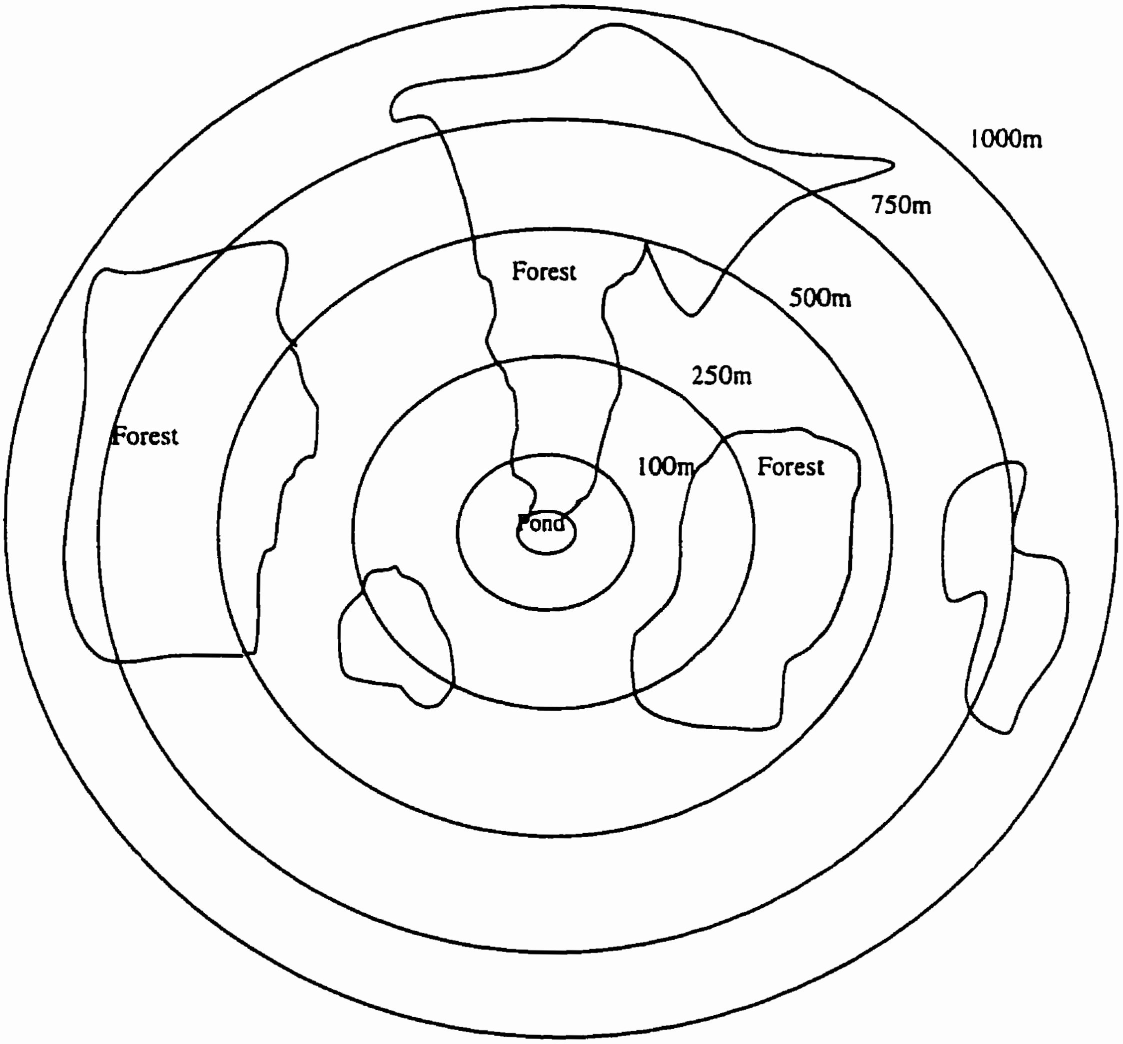

Figure 2-1. Schematic diagram depicting the configuration of the concentric circles and the distance classes used in the analysis of the incidence of *Ambystoma maculatum* at ponds (Diagram not to scale). Small scale: 100 m and 250 m distance classes, medium scale: 500 m distance class, broad scale: 750 m and 1000 m distance classes.

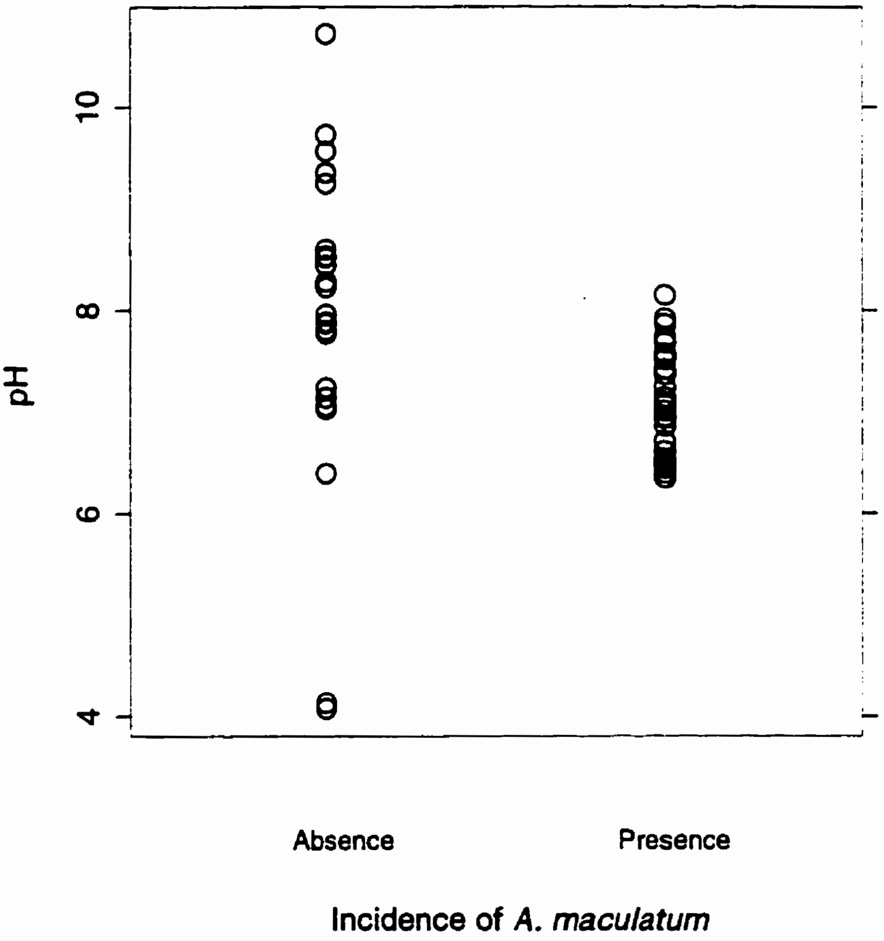

Figure 2-2. Relationship between the pH and the incidence of *Ambystoma maculatum*. Each dot represents a pond (n=56). pH ranges from 4.3 to 10.63.

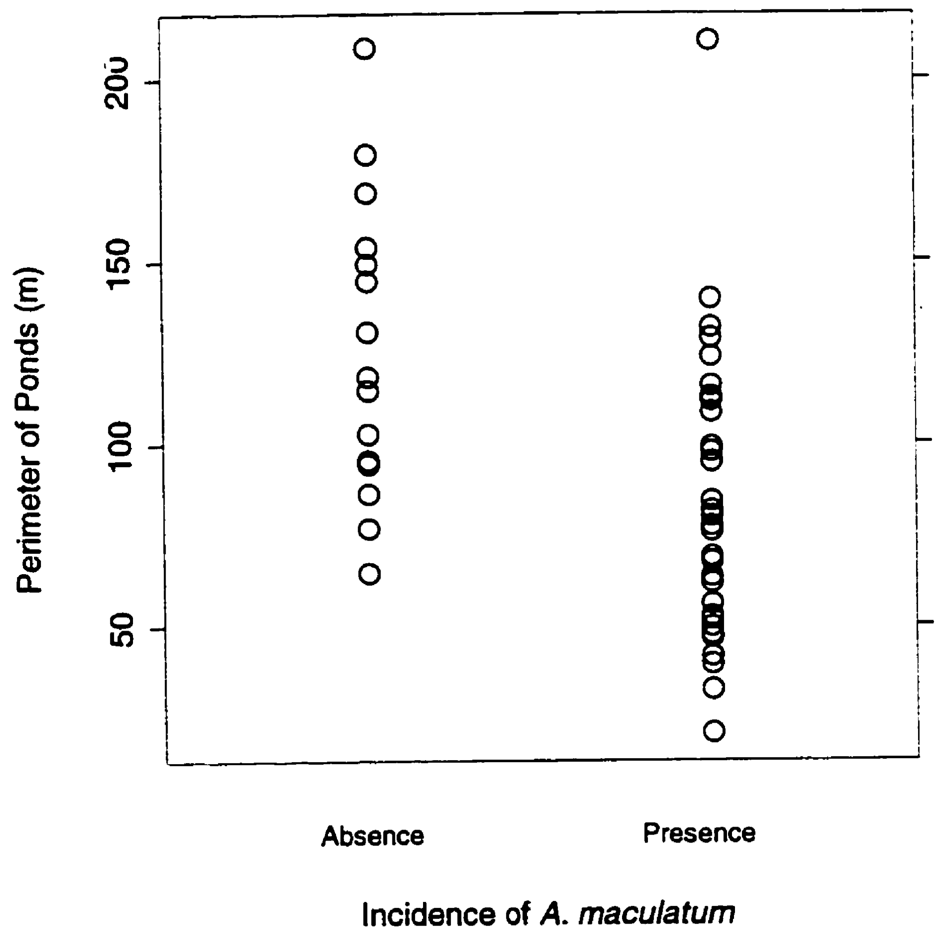

Figure 2-3. Relationship between the perimeter (m) and the incidence of *Ambystoma maculatum*. Each dot represents a pond (n=47).

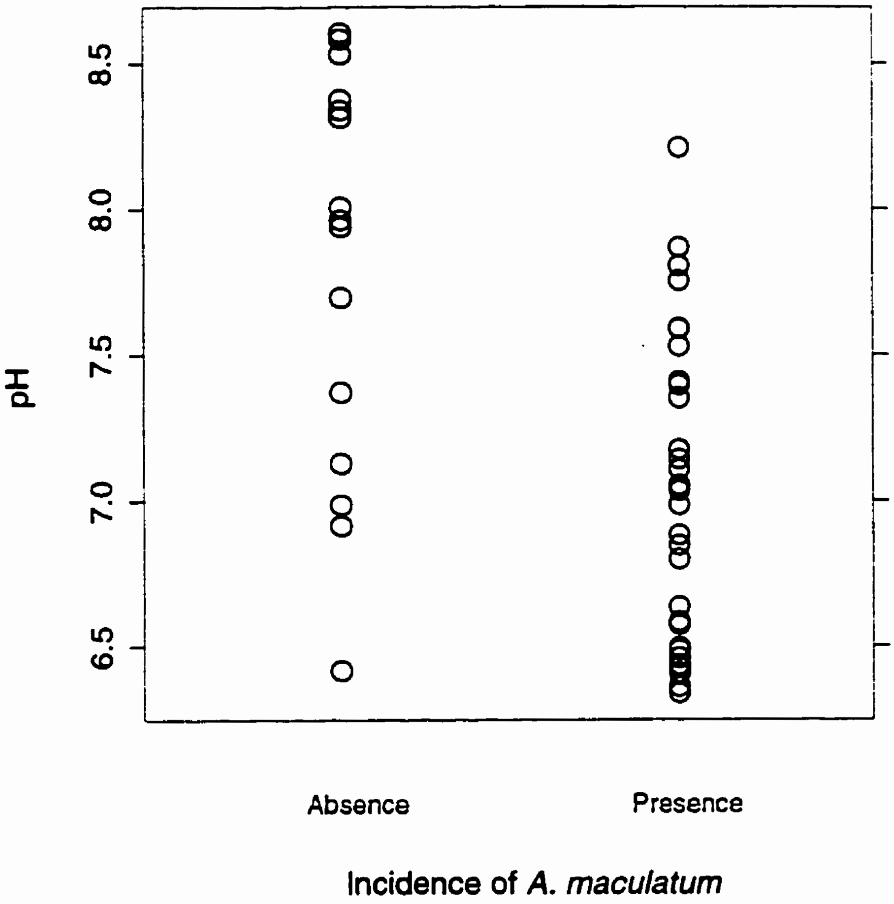

Figure 2-4. Relationship between the pH and the incidence of *Ambystoma maculatum*. Each dot represents a pond with pH greater than 6 and less than 8.7 (n=47).

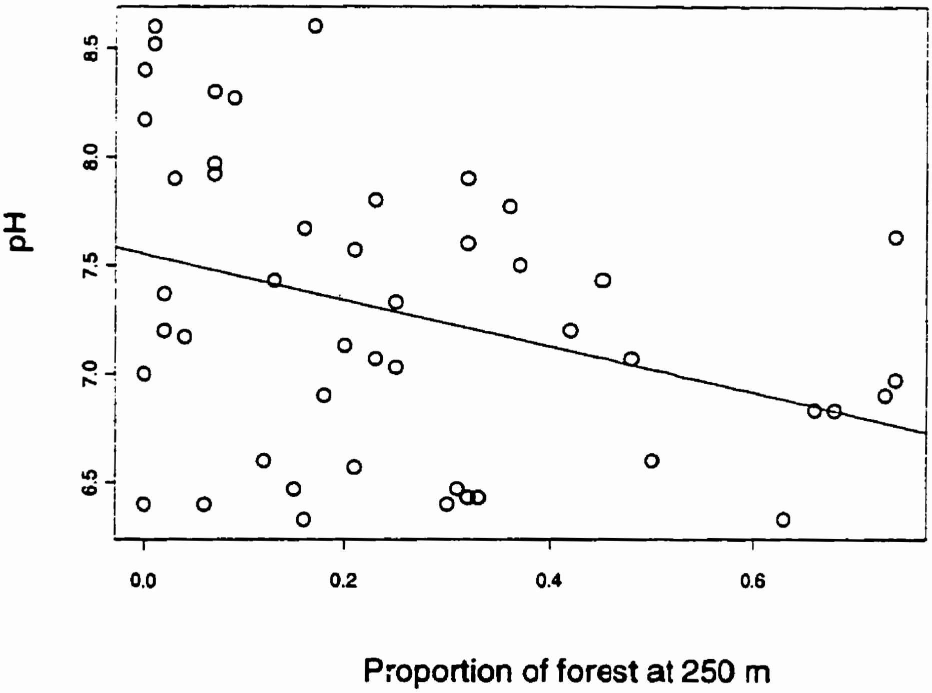

Figure 2-5. Significant negative linear relationship between the proportion of forest at 250 m and pH ($n = 47$). Regression coefficient was -1.067 for forest and an R^2 of 0.121.

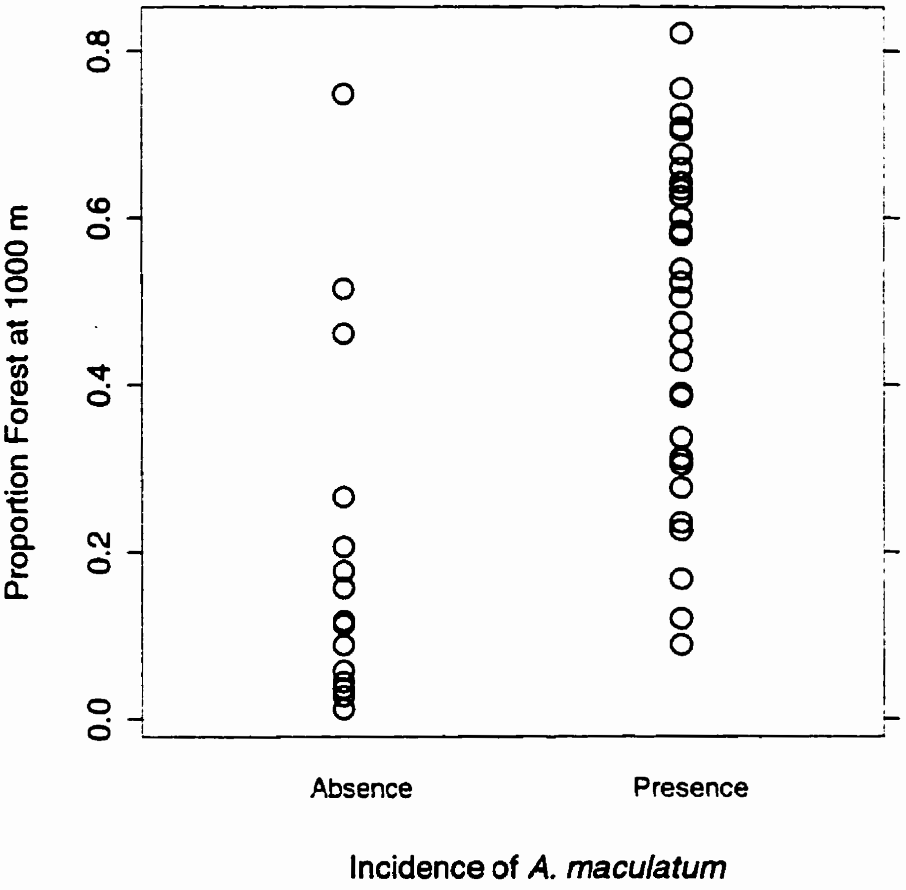

Figure 2-6. Relationship between the proportion of forest 1000 m from a pond and the incidence of *Ambystoma maculatum*. Each dot represents a pond.

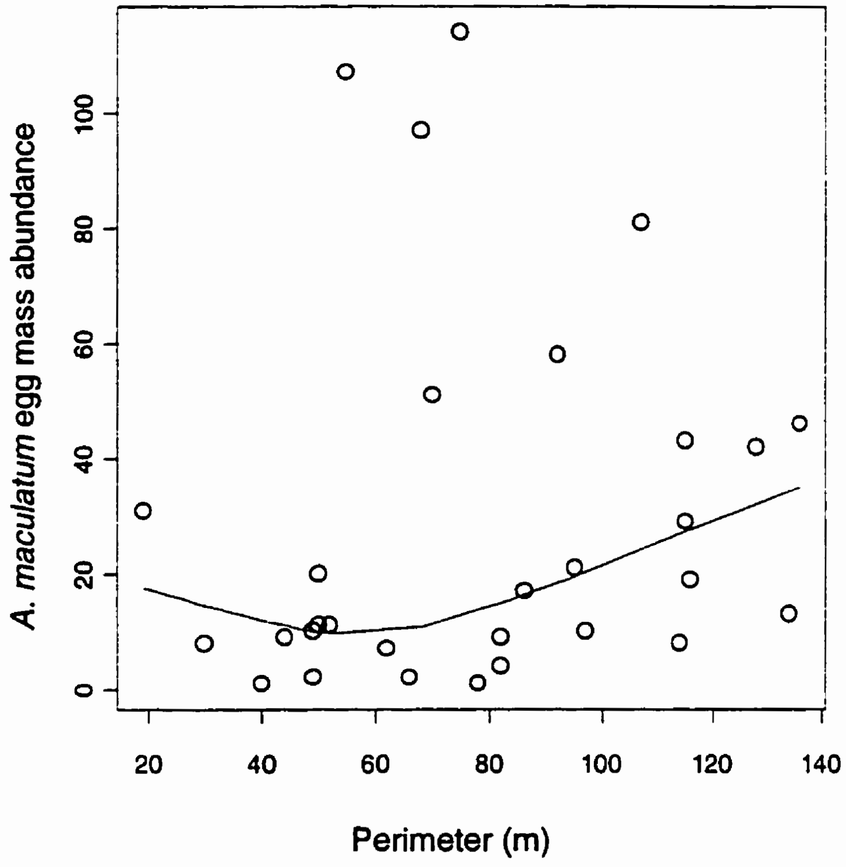

Figure 2-7. Relationship between the perimeter of ponds (m) and the abundance of *Ambystoma maculatum* egg masses. Each dot represents a pond (2 ponds with highest abundance excluded from plot). Locally weighted regression line fit to the data.

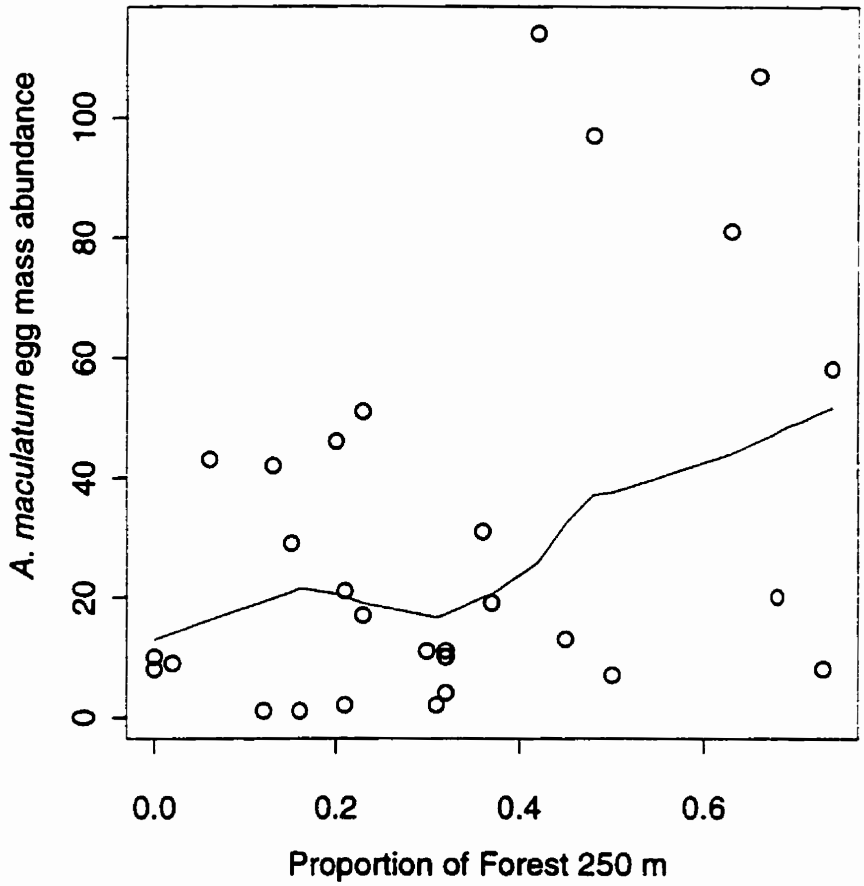

Figure 2-8. Relationship between the proportion of forest at 250 m and the abundance of *Ambystoma maculatum* egg masses. Each dot represents a pond (2 ponds with highest abundance excluded from plot). Locally weighted regression line fit to the data.

Chapter 3. The effects of habitat type on the movement of juvenile *Ambystoma maculatum*.

Introduction

Movement is the process that mediates the effects of changes in landscape structure on populations of organisms (Wiens 1997) and is important in the spatial structuring of populations (Taylor 1997). Within a spatially structured population it is understood that dispersal is the process that "connects" local populations (Vos and Chardon 1997; Sjögren-Gulve 1998b; Johst and Brandl 1997) (as discussed in Chapter 2). Without movement between populations the potential for local extinctions increases and the probability of persistence, for a network of populations decreases (Sjögren 1991).

For many amphibian species it is known that juveniles are the primary dispersers (see Breden 1987; Schroeder 1976; Dole 1971; Gill 1978; Berman and Saproznikov 1994; Shoop 1974). To determine if juvenile dispersal is the process responsible for "connecting" local populations and contributing to the spatial structuring of populations, an understanding of the direction of initial emergence movements, and the extent and ability of juvenile dispersal movements are essential.

The direction of juvenile movement from natal sites can have important implications for the persistence of a spatially structured population (Sjögren-Gulve 1998b). Non-random, or target-oriented, movement can negatively affect population persistence because it decreases the probability of colonization or recolonization (Sjögren-Gulve 1998b). Knowledge of the extent and ability of juvenile movement through different habitat types is important for understanding the effect of changes to landscape structure on populations of *A. maculatum*.

A common approach to obtaining information on the broader scale movement of organisms (i.e. not movement pathways) is through a mark-recapture study. Toe clipping is one of the techniques used in mark-recapture work (see Shoop 1974 and 1968; Woodward 1982). It is possible that toe clipping could affect the movement behaviour of an individual, however few studies have explored this experimentally or discussed the potential impacts these procedures could have on their results.

There is little known about the movement abilities of juvenile *A. maculatum* (Shoop 1974), or the sub-adult stage, which can range from two to six years of age (Flageole and LeClaire 1992). This lack of information is primarily due to difficulties associated with sampling and tracking these individuals (Shoop 1974). In Chapter 1, I determined that the post-breeding departure movements of adult *A. maculatum* were non-random, that they were directed towards forest. In this study I examine the direction of the initial emergence movements of juvenile *A. maculatum* from ponds to determine if they are directed, i.e. target-oriented. I also examine, experimentally, the effects of toe clipping and habitat type (forest or field) on the rate of recapture and the rate of movement for juveniles released within an enclosure.

Methods

Survey

A survey of juvenile *A. maculatum* was conducted at 6 of the 10 ponds where adults had been sampled in Chapter 1 from 5 August - 14 November 1997 (101 days). Emerging juveniles were intercepted at drift fences as they moved out of their natal pond. The trapping technique was the same as that described in Chapter 1, however, the side-flap pail trap (Nadorozny and Barr 1997) was modified because the juvenile *A. maculatum* were small enough to escape through the mesh. A finer mesh was placed over the side-flap pail trap window and door. A total of 24 fences and 105 traps were used and each pond had a minimum of three partial drift fences. Each fence was categorized by the immediate habitat in which the fence was erected as a forest or a field fence.

All traps were checked at least every second day, depending upon the weather conditions. The presence of an individual at a trap and the snout-vent length (svl) was recorded and individuals were released in moist vegetation away from the fence. At one pond juveniles were kept when required for use in the following experiments. They were maintained in an enclosed bucket with moist vegetation until the required time of use in the experiment. Individuals were never kept more than 24 hours and no individuals were displaced. For all experiments they were released in habitat adjacent to their natal pond.

Emergence

At each pond, the total numbers of juveniles captured at forest fences and the total number at field fences were tallied. The total length of fencing in each habitat type was also recorded and the proportion of this fencing that was located in forest was calculated. The direction of the emergence movements of juveniles, in relation to forest, was examined using a generalized linear model, with Gaussian distributed errors. The response variable was the arc sin square root of the proportion of individuals captured at a forest fence and the predictor variable was the proportion of the fencing that was in forest. To account for the variation in numbers of juveniles trapped at each pond the model was weighted by total number of juveniles per pond. Analyses were conducted using S-plus statistics package (StatSci 1995) and results tested against an F distribution, with a type I error rate of 5 percent.

Enclosure Experiments

The following experiments were conducted to examine the effects of toe clipping on the rate of recapture and on the rate of movement of juveniles as well as the effects of habitat type within which individuals were released. Four 2 x 2 m enclosures with a side-flap pail trap (Nadorozny and Barr 1997) in each corner were constructed, two in forest habitat and two in agricultural field habitat. Enclosures were constructed in forest and field habitats adjacent to the pond at which juveniles, used in the experiments, had been trapped.

Juvenile *A. maculatum* were collected from the traps at the partial drift fences as they emerged out of the pond, as described above. For each of three trials and four enclosures, two juveniles with one back toe clipped and two with no toes clipped were released in the center of the enclosure after 11:00 pm. Traps and the sides of the fences were checked approximately every 15 minutes and the time-to-recapture was recorded. If an individual was not captured within the first 24 hours, the traps were checked the following day. Trials were conducted on three different evenings using a total of 48 individuals.

To examine the effects of toe clipping and habitat type on the recapture rate of juveniles a logistic regression analysis was used, with the binary response variable recaptured versus not recaptured. The experimental design was completely balanced, therefore the main effects and all possible interactions were fit in this model. The main effect terms are date of trial, enclosure number, clipped or non-clipped and habitat type (forest or field) and these were fit first, followed by all possible interactions.

The effects of toe clipping and habitat type on the rate of movement of juveniles, was examined using a generalized linear model, with Gaussian distributed errors. The response variable was the log transformation of the time-to-recapture (in minutes). To enable an analysis with a completely balanced design, all individuals were incorporated in this analysis, recording the time-to-recapture for those not recaptured as the maximum amount of time-to-recapture plus one. Again all main effects of date of trial, enclosure number, clipped or non-clipped and habitat type (forest or field) were fit first, followed by all possible interactions. Analyses were conducting using S-plus statistics package (StatSci 1995), with a type I error rate of 5 percent.

Results

There was no significant effect of the proportion of forest fencing on the proportion of individuals caught at forested fences (p-value = 0.232). This indicates that juvenile emergence movements are not directed towards forested habitat.

Toe clipping had no significant effect on the recapture rate of juveniles (p-value = 0.098) and no significant effect on the time-to-recapture of juveniles (p-value = 0.224) (Figure 3-1). This suggests that the clipping of one back toe does not influence movement for juveniles. There was a significant effect of habitat type on recapture rate (p-value = 0.002). There was a 46 % recapture rate in the forest and 83 % in the field enclosures. There was also a significant effect of habitat type on time-to-recapture (p-value = <0.001). Figure 3-2 illustrates that the time-to-recapture was greater in the forest than in the field indicating that the rate of movement of juveniles was greater in field than forest (Figure 3-2).

Discussion

The emergence movements of juvenile *Ambystoma maculatum* were not significantly influenced by the total amount of forested fencing, suggesting that their emergence movement is not directed towards forested habitat (i.e. random). This is contrary to other research on juvenile amphibians which has shown non-random or target-oriented dispersal movements (see Sjögren-Gulve 1998a, pool frogs (*Rana lessonae*). In my previous study adult *A. maculatum* showed directed post-breeding movements towards forested habitat (Chapter 1). Adults of several other amphibian species also exhibit these non-random, or target-oriented movements, including the adult leopard frog (*Rana pipiens*) (Dole 1971), pool frog (*Rana lessonae*) (Sjögren-Gulve 1998a), striped newts (*Notophthalmus perstriatus*), eastern narrow-mouthed toads (*Gastrophryne carolinensis*) (Dodd and Cade 1997). Random dispersal increases the probability of colonization or recolonization and thus has a positive effect on the persistence of spatially structured populations (Sjögren-Gulve 1998b). It is possible, however, that directed emergence movement was not detected because of a small sample size and thus lack of statistical power.

It is known that juvenile *A. maculatum* can move through field habitat because Gibbs (1998b) anecdotally observed recently metamorphosed juvenile *A. maculatum* travelling across open lands towards forested habitat. Field habitat is not ideal for *A.*

maculatum because of dry environmental conditions and a greater exposure to predation (Madison 1997). Shoop (1974) observed high mortality (due to desiccation) in juvenile *A. maculatum* that had initially emerged into field habitat, but that had not moved away from the edge of the pond. This suggests that, given suitable environmental conditions to avoid desiccation, juveniles have the ability to cross open habitat (Ray 1958).

I determined that juvenile *A. maculatum* move more in field habitat than forested habitat. In field habitat, a greater rate of movement may be necessary to decrease the probability of mortality while moving to find suitable habitat. It is also possible that the rates of movement are lower in the forest because this is suitable habitat with sufficient moisture and cover material (i.e. leaf liter) and therefore the stimulus to move to appropriate habitat is low.

A juvenile's ability to move through field habitat is important for a spatially structured population because it suggests that, although the presence of fields may decrease the probability of successful dispersal, it does not act as a complete barrier to movement. A faster rate of movement within field may enable access to forest at greater distances from the natal pond.

Future work should also encompass tracking where movement pathways through habitats can be examined in particular the success of movement of juveniles through fields. I determined that there were no negative effects of toe clipping on the movement of juvenile *A. maculatum* and thus mark-recapture methods could be employed and movement results interpreted with confidence.

Dispersal of juveniles may be the process that "connects" populations of *A. maculatum*, however, there is little known about the movement abilities of juvenile *A.*

maculatum (Shoop 1974) or the sub-adult stage, which can range from two to six years of age (Flageole and LeClaire 1992). For many amphibian species it is recognized that juveniles are the primary dispersers. Breden (1987) determined that juvenile Fowler's toads (*Bufo woodhousei fowleri*) moved greater distances than adults and Schroeder (1976) and Dole (1971) determined that for green frogs (*Rana clamitans*) and leopard frogs (*Rana pipiens*), respectively, juveniles were the primary dispersers. Berman and Sapozhnikov (1997) found with the Siberian salamander (*Salamandrella keyserlingii*) only immature individuals and those born in the current year were trapped in areas away from breeding sites, some greater than a kilometer away from a pond.

It is interesting to note that the life histories of juvenile *A. maculatum* is comparable to the juvenile red spotted newt, (*Notophthalumus viridences v.*) which has a terrestrial red eft stage (3 to 4 years) as does *A. maculatum* (Gilhen 1984; Gill 1978; Hurlbert 1970; Healy 1975). Gill (1978) determined that it was the juvenile stage (red eft) that moved the greatest distances and that they were primarily responsible for colonization and recolonization within the metapopulation. For *A. maculatum* populations, more knowledge of the movements of juveniles and sub-adults is required before it can be definitively stated that the process of movements during these phases is the primary mechanism responsible for the spatial structuring of these populations.

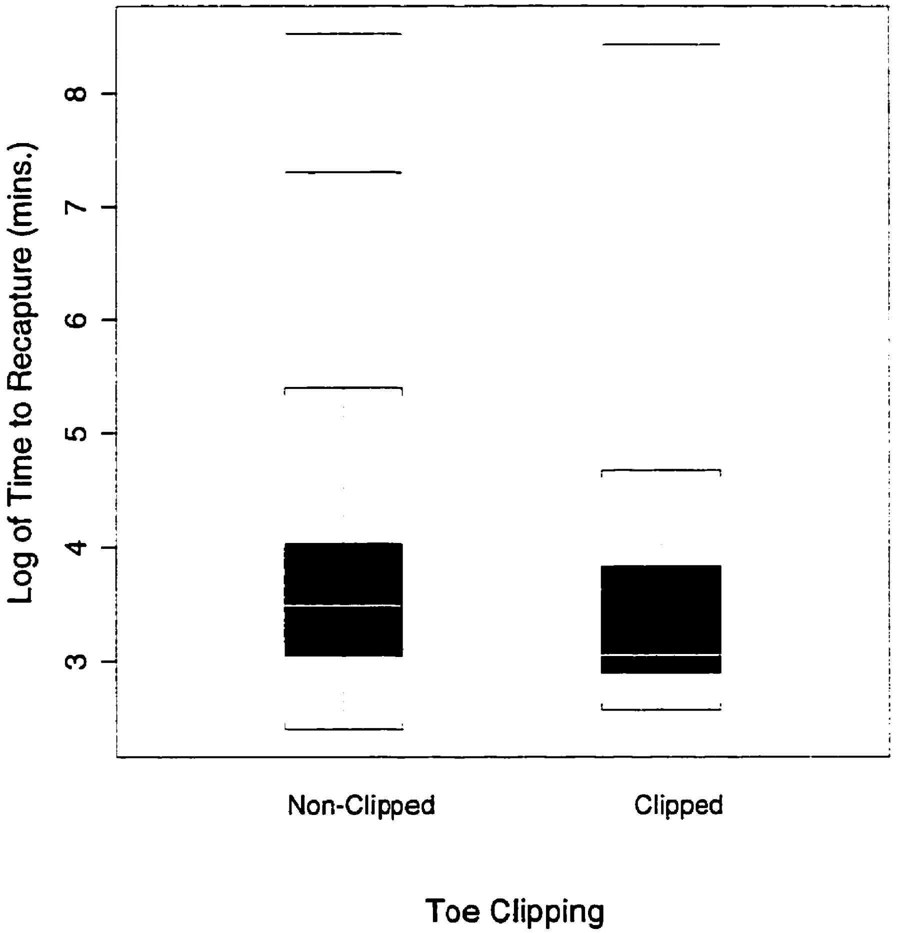

Figure 3-1. Box plot showing median (white line), interquartile range (box), range (whiskers), and outliers (bars) of the log of time until recapture for toe clipping of *Ambystoma maculatum*. The difference is not statistically significant (p-value = 0.22).

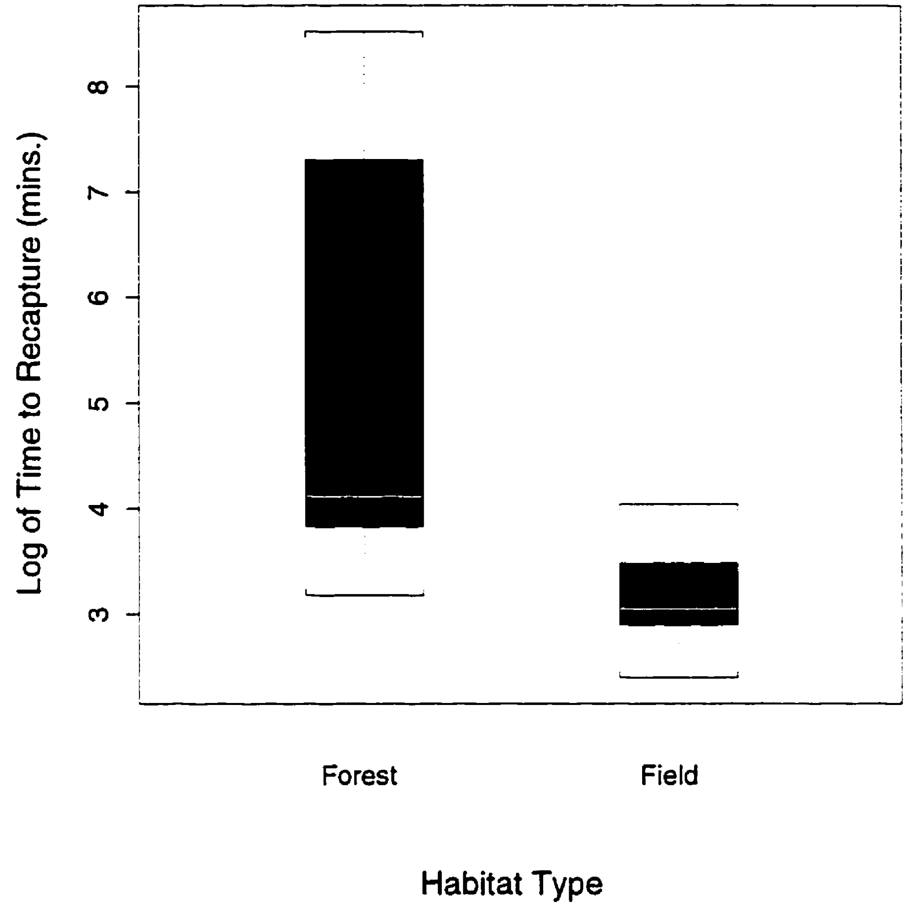

Figure 3-2. Box plot showing median (white line), interquartile range (box), range (whiskers), and outliers (bars) of the log of time until recapture (minutes) for *Ambystoma maculatum* released in forest versus field habitats. Statistically significant difference (p-value = 0.005).

Chapter 4. Harmonic radar: a new method for tracking amphibians

Introduction

Animal movement is important to the demographics and the genetics of populations (Merriam 1991). For amphibians, knowledge of movement abilities and movement pathways can be acquired through a number of different tracking methods, each varying in effectiveness, feasibility, and success. Tracking small amphibian species and juveniles of some amphibian species however, is more difficult. For many amphibian species, juveniles are the primary dispersers (see Breden 1987; Schroeder 1976; Dole 1971; Gill 1978; Berman and Saproznikov 1994; Shoop 1974). There is little known about the movement abilities of juvenile yellow-spotted salamanders, *Ambystoma maculatum* (Shoop 1974). Juvenile *A. maculatum* weigh, on average, 0.8 g and are approximately 50 mm in snout-vent length and there are few tracking techniques available for an organism this size and therefore little tracking work has been conducted.

In a review of tracking techniques for amphibians, Ferner (1979) discussed the value of radioactive tagging for tracking organisms that are too small for a radio transmitter used with radiotelemetry. Using low level radioactive cobalt as a radioactive tag, Hardy and Raymond (1985) successfully tracked *Ambystoma* species, and Kleeberger and Werner (1983) and Douglas and Monroe (1981) successfully tracked adult *A. maculatum*. Semlitsch (1981) implanted radioactive Ta-182 wire tags and was also successful in tracking some *Ambystoma* species. There are however, safety, feasibility, and invasiveness concerns associated with radioactive tagging. Radiotelemetry also has been successfully used to track amphibian species (Madison 1997; van Nuland and Clause 1981), however there are some disadvantages to radiotelemetry, such as the complexity, cost per transmitter, feasibility, and weight (Ferner 1979).

There are other methods of tracking used with amphibians that enable finer resolution of movement pathways to be measured. These include, thread bobbins (Wilson 1994; Dole 1965) and fluorescent yarn tags or fluorescent capsules, which leave a fluorescent trail of the organism's movement pathway (Windmiller 1996). These have certain advantages in their simplicity, low cost and use with small amphibians (Windmiller 1996). Harmonic radar provides an alternative method that has been successfully used in tracking insects (Roland *et al.* 1996; Mascanzoni and Wallin 1986). The tags are small and light, have a long life span and low cost.

Harmonic Radar Technology

The harmonic radar technology used was from RECCO Rescue Systems, Lidingo, Sweden (http://www.recco.com, 1999). It consists of a hand held transmitter-receiver unit with a Yagi antenna that transmits a 1.7 Watt continuous microwave frequency of 917 MHz and a reflector tag that consists of a diode and a wire antenna (Roland *et al.* 1996). The reflector tag is a passive device consisting of a Schottky diode attached to an antenna wire of a specific length. The antenna wire absorbs power from the 917 MHz radar waves and passes this on to the diode where the signal is re-radiated at a harmonic frequency of 1834 MHz, double that of the transmitted wave (Mascanzoni and Wallin 1986). The RECCO unit was originally developed for use in locating avalanche victims, where a reflector tag is attached to a skier's boot. It is the configuration of this reflector tag that has been modified and reduced in size to be used in the tracking of small organisms.

The harmonic radar technique, with the RECCO detection system, was successfully modified by Roland *et al.* (1996) for use with the Apollo butterfly, common alpine butterfly, larvae and moths of the forest tent caterpillar and a parasitic tachinid fly. Their reflector tags weighed 0.4 mg, with a 8 cm dipole antenna and had a detection range of 50 m (Roland *et al.* 1996). Mascanzoni and Wallin (1986) also successfully used this system for tracking carabid beetles. The two reflector tags they used weighed approximately 0.08 g and 0.03 g and they experimented with the antenna lengths and determined that a maximum detection distance of 13 m could be obtained with a 10-13 cm antenna. Reflector tags constructed for the tracking of insects are microscopic and are therefore relatively expensive and difficult to make.

The objective of this study was to develop an inexpensive, light weight reflector tag for use with the RECCO harmonic radar technology to track the terrestrial movements of juvenile *A. maculatum*. A second objective was to determine if the attachment of the reflector tag affected the rate of movement of juvenile *A. maculatum*.

Methods

Reflector Tag Construction

There are several different Schottky diodes that can be used, varying in size, weight, shape, and cost (see an electronics supply catalogue). I used a HP HSMS-2830, L30 Schottky diode, with the L30 indicating low profile bulk (i.e. surface mount casing), an advantage in decreasing both its size and weight. I used a 36-gauge, enameled copper wire for the dipole antenna that was soldered to the diode with utecktic solder, but in general, the antenna does not have to be copper, nor 36 gauge. What is important, is that the antenna is of a specific length, equivalent to a proportion of the wavelength of the radar signal. The longer the antenna, the greater the detection range. Through trial and error, I determined the optimal configuration to be a 15.75 cm dipole antenna consisting of 2.25 cm of the antenna wire soldered to the positive pole, or lead, of the diode and 13.5 cm soldered to the negative pole (Figure 4-1). The optimal configuration however, can vary depending on the soldering, the type of diode used, or the type of wire used for the antenna, and the antenna orientation and configuration. Therefore, it is extremely important that a thorough period of trial and error be conducted in order to determine the ideal antenna configuration. Some configurations of the antenna were eliminated immediately because they were not feasible with the small, terrestrial *A. maculatum* juveniles. Examples of these configurations include, an antenna of a length greater than 16 cm total length, or a configuration with antenna wires of equal length extending from each pole of the diode (as was used by Roland *et al.* (1996)).

Since there is no unique frequency per individual reflector tag, a label with a unique alphanumeric code was glued to each diode. Furthermore, the tracking of juvenile *A. maculatum* occurred at night so to aid in the re-location and retrieval of individuals a fluorescent powder was painted on to the antenna wire. Using a UV light this fluorescent powder enabled the individuals to be re-located with ease. A one cm loop of thread was glued, using crazy-glue, to the back of the diode as a point of attachment of the reflector tag on to the individual. The reflector tag was attached to the dorsal surface of the base of the tail of juvenile *A. maculatum* with a suture. The diode was encased in a coating of epoxy to ensure protection of all solder joints and the loop.

The individual diodes weigh 0.0094 grams and the reflector tag (diode, solder, epoxy, and antenna wire) weighs 0.03 g. At one meter above the ground, the detection range for the 15.75 cm antenna was greater than 50 meters. The detection range for this antenna (15.75 cm) at ground level, however, was approximately 14 meters. With a shorter antenna (8 cm) the range decreased to approximately 7 m.

The signal, and thus detection range, was greatest when the reflector tag was away from the ground because minerals and water in the soil absorb much of the transmitted energy. The reflector tag does not work if submerged in water. The signal can be affected by metal objects or electrical equipment or by anything in the air that interrupts the flow of the signal, including rain. Diodes cost approximately one dollar Canadian. The RECCO transmitter-receiver detection unit is relatively expensive but can be rented on a monthly basis.

Field Trials and Experiment

Juvenile *A. maculatum* were collected in pitfall traps in August of 1997 at six agricultural ponds located in the Annapolis Valley, Nova Scotia, Canada (45°05'N; 64°30'W) (Appendix 1). Individuals were brought into the lab and the reflector tags were sutured into place, via the thread loop on the reflector tag, using one suture through the muscle at the base of the tail on the dorsal surface. In test trials, four individuals were released, on three different nights (n = 12), at their point of capture adjacent to the pond the following night and were located every 15 minutes for three hours.

An experiment was also conducted to determine the effects of reflector tag attachment on the movement of juvenile *A. maculatum* in forest habitat and field habitat enclosures by measuring the rate of recapture of tagged and non-tagged individuals. Four 2 x 2 m enclosures with a trap in each corner were constructed, two in a field habitat and two in forested habitat. Juvenile *A. maculatum* were collected and for each trial two with a reflector tag attached with a suture (as described above) and two without a reflector tag attached were released in the center of each enclosure after 11:00 pm. This was conducted on two different nights with a total of 32 individuals. There were four different enclosures and four individuals released per evening, two per habitat type. Traps and the sides of the fences were checked every 15 minutes and the time-to-recapture was recorded.

A linear regression analysis was used to determine if there was an effect of date, enclosure, and the presence or absence of a reflector tag on the log transformed response variable time-to-recapture (minutes). The effect of habitat type (forest versus field) on the time-to-recapture was also examined within this linear model by including a habitat term. All statistical calculations were conducted using S-plus statistics package (StatSci 1995), with a type I error rate of 5 percent. Individuals that were released but became entangled were omitted from the analysis. As well, individuals that were not recaptured within the same evening of release were omitted.

Results

The juveniles tracked in the trials did not move more than 5 meters from the point of release. Fifty percent (6 of 12) of these individuals became entangled when the antenna wire became twisted around vegetation and in one case the sutures pulled out and the loose tag was recovered.

Within the field enclosures 4 of the 32 individuals released with reflector tags attached were not recaptured at the fence or in traps because the antenna wire became entangled in the vegetation. Four of the individuals released in the forest were not recaptured within the same evening and two of these had reflector tags attached and two did not. When the antenna wire did not become entangled in vegetation, there was no significant effect of the presence of the reflector tag or of any other effects on the rate of movement (Table 4-1; Figure 4-2).

Discussion

I have successfully modified a cheap, light weight reflector tag. However, there are some limitations to the application of the harmonic radar technology to the tracking of juvenile yellow-spotted salamanders (*A. maculatum*). I experienced two primary problems with the attachment of the reflector tag to the juvenile *A. maculatum:* 1) the antenna wire became tangled in the vegetation and 2) the suture would pull out of the tissue in the tail. With a slightly larger amphibian species, or one that lives in a habitat with less vertical structure, or by using a different method of attachment, or a different reflector tag construction this problem could be alleviated. Recently, Madison (1997) successfully implanted radio transmitters to track *A. maculatum*. It is possible that the reflector tag configuration of the antenna wires could be modified or adapted, as described previously. One of the primary differences between Madison's (1997) work and the potential implantation of the reflector tags, however, is that the radio transmitters do not have an external antenna. There is the opportunity for modifications to this design through trial and error and further experimentation. For example, to decrease the potential for becoming tangled, a finer wire or stiffer wire, depending on the habitat, could be used. Also, the fluorescent paint used in these experiments created a rough surface on the antenna wire and it is possible that this increased drag and reduced flexibility, thus contributing to our problem with entanglement and sutures pulling out. Again, depending on the size of the animal and habitat type the dragging antenna wire could be less of a problem.

There are some limitations to the use of harmonic radar. These include a limited detection range, the inability to use it in water, and the decrease in detection range when below the ground. An appropriate search pattern however, could alleviate many of these concerns with the detection range. If search times were frequent enough to ensure that no extreme distances were traveled between checking then. This method can be used to track the terrestrial phase of many amphibian species. It is often the terrestrial phase of amphibians where information on their movements and resource requirements is lacking.

There are advantages to this technique that out weigh its limitations, such as, the small size and weight, the low cost and the long life span of the individual reflector tags. Although some species-specific modifications may be necessary, harmonic radar is a promising, new method for tracking the terrestrial phases of amphibian species. This will provide the opportunity for more information of juvenile movement and dispersal to be determined and thus contribute to the understanding of the role of juveniles in the spatial structuring of populations of *A. maculatum*.

Table 4-1. Analysis of variance examining the effects of the attachment of reflector tag on the movements of juvenile *Ambystoma maculatum*. The response variable is the square root of time-to-recapture (minutes).

Term	df	MS	F	p(F)
Date	1	2.790	0.962	0.339
Enclosure	1	0.158	0.055	0.818
Reflector Tag	1	3.351	1.156	0.296
Habitat	1	3.107	1.072	0.314
Habitat x Reflector Tag	1	2.068	0.713	0.409
Residuals	19	2.899		

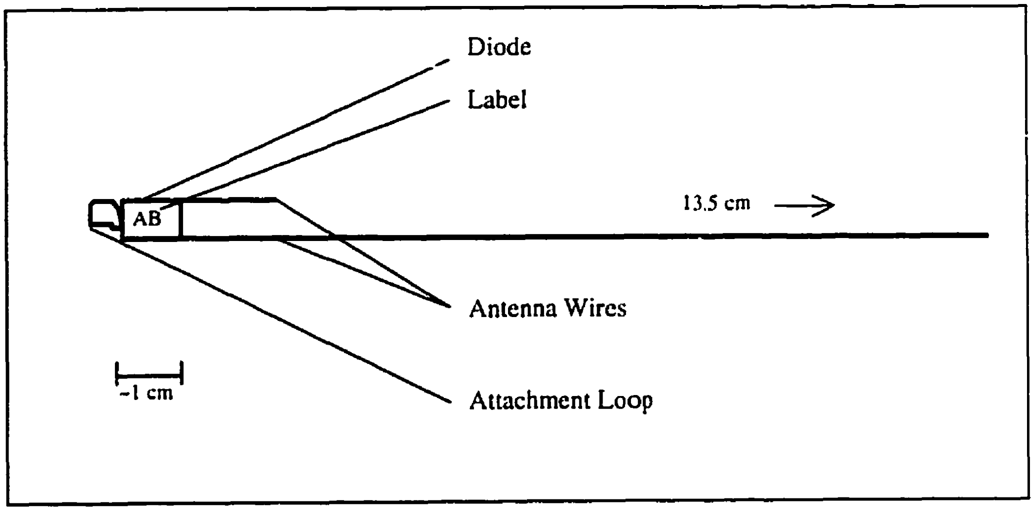

Figure 4-1. Schematic of reflector tag, consisting of diode, antenna wires, and attachment loop.

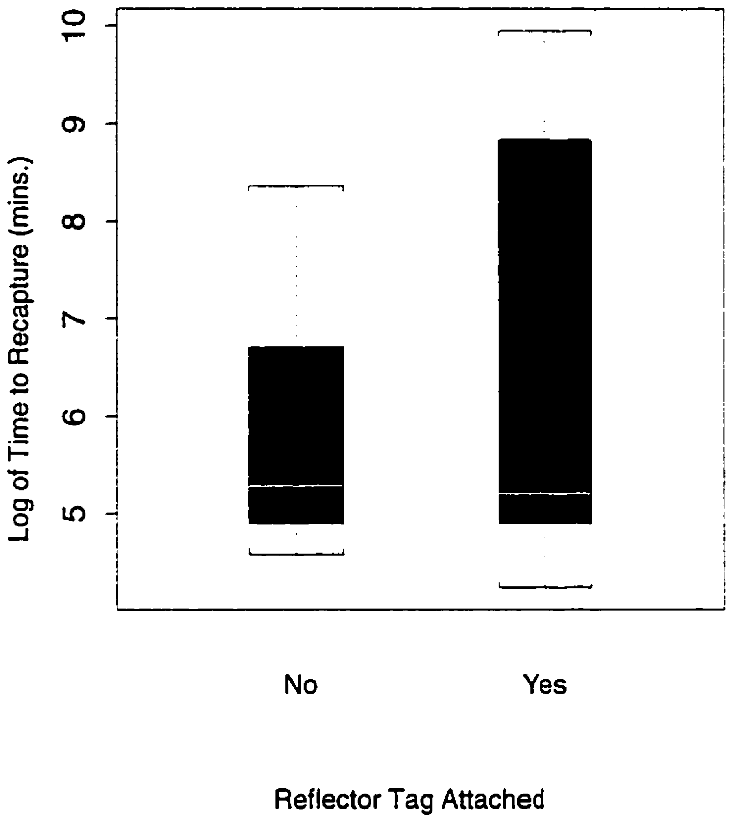

Figure 4-2. Box plot showing median (white line), interquartile range (box), range (whiskers), and outliers (bars) of the log of time until recapture (minutes) for *Ambystoma maculatum* with and without reflector tag attached. Difference not statistically significant (p-value = 0.41).

General Discussion

In this thesis I determined the spatial extent of the effects of the proportion of forest on populations of yellow-spotted salamanders (*Ambystoma maculatum*) using a multiple scale approach, and a suite of analyses. I used incidence and abundance as indirect measures of adult movement and showed that the proportion of forest is important at both small and large spatial scales. I also showed that local populations of *A. maculatum* exist as a network of populations, as part of a spatially structured population.

In Chapter 1, I determined that the proportion of forest immediately surrounding the breeding site influences incidence and density for local populations. This analysis revealed a threshold amount of forest at 15%, where below this amount of forest *A. maculatum* were not present at ponds. This finding concurs with other research on threshold effects (Gibbs 1998a; Andrén 1994) and provides further indication of the critical interaction between landscape structure, the distribution of resources and the movement of an organism between resources, and local population persistence.

I demonstrated, in Chapter 2, that the proportion of forest influences incidence and abundance at the broadest spatial scale examined. Roads, at a small spatial scales, had a negative effect on incidence and abundance and therefore potentially decrease the connectivity of the landscape. I concluded that an increase in the amount of forest results in an increase in the connectivity of the landscape for multiple populations of *A. maculatum*. From determining this connectivity for *A. maculatum*, and from the results in Chapter 1, I concluded that populations of *A. maculatum* are spatially structured at an extent of at least 1000 m. The identification of spatial structure in a population is important in the understanding of the degree to which changes in the landscape may affect a species. There has been an increase in the incorporation of spatial theory when examining populations of organisms (Steinberg and Kareiva 1997). Understanding the spatial structure of populations can play a critical role in the development of conservation and management strategies (Semlitsch 1998b) and in the determination of important future ecological research.

Movement is the process that mediates the effects of changes in landscape structure on populations (Merriam 1991; Kareiva 1990; Taylor 1997). I too identified movement as the primary process through which the effects of changes to landscape structure impacted local populations and the spatial structuring of populations of *A. maculatum* persistence. In addition to its role in maintaining persistence in local populations movement contributes to the persistence of a network of populations through the "rescue" effect, colonization, or recolonization (Merriam 1991; Hansson 1991).

Dispersal, is recognized as the process that "connects" local populations, thus contributing to the spatial structuring of populations (Kareiva 1990; Vos and Chardon 1997; Sjögren-Gulve 1998b; Johst and Brandl 1997). Through experimentation described in Chapter 3, I explored the movement capabilities of juvenile *A. maculatum*, since for amphibians, it is juveniles that are often the primary dispersers. I determined that juvenile rate of movement was affected by habitat type, with individuals moving faster in field habitat. If juvenile dispersal is indeed random, as determined in Chapter 3, and an individual disperses into a field, this accelerated rate of movement may enable successful dispersal to a distant suitable habitat. This information provides some insight into the role of juveniles by increasing our understanding of their movement capabilities, however, there is still a need to understand their movements in more detail. Despite similar approaches, there was a discrepancy in the detection of an effect of habitat in Chapters 3 and 4. The experiments for each of these chapters were conducted on different nights and it is possible that environmental conditions may be affecting the rate of movement, thus leading to such a difference in the detection of an effect of habitat. If this is the case then it indicates that weather variables should perhaps have been included in the analyses, and that greater sample size may be necessary to truly elucidate the effects of habitat on the rate of movement of juveniles. In Chapter 4, I describe the development and trials of a new technique with potential for tracking the movement pathways of juveniles.

To fully understand the dynamics of *A. maculatum* populations, both at the small and broad scale, there are some other characteristics and abilities of this organism that must be determined. A greater understanding of the movement abilities of juveniles, and the effects of changes to landscape structure on these movements, is critical to fully understanding the interaction of landscape structure, movement and population persistence. Knowing the rate of local extinctions would also provide insight into the movement of individuals between local populations, however, I did not determine the rate of local extinction. Nor did I determine the age structure of populations that could provide an indication of the probability that a population will persist.

A. maculatum can live to be 28 years of age (Flageole and LeClare 1992) and therefore it is possible that not all breeding populations are viable. Local extinctions could be masked by the longevity of a species because small populations may not be viable yet may persist for long periods simply because of the longevity of individuals (Saunders *et al.* 1991). Therefore the presence of breeding individuals does not signify a guarantee of continued persistence (Saunders *et al.* 1991) and with a long-lived species the negative effects of landscape structure could be under estimated. Therefor there is a need to obtain data on the age structure of populations and rates of local extinction prior to reaching any conclusions on the persistence of the spatial structuring of populations.

Results from this thesis illustrate the importance of a multiple scale approach to ecological research. Without incorporating multiple spatial scales the presence of spatial structuring of *A. maculatum* populations would not have been detected because it was the presence of the landscape effect at 1000 m that revealed this. The sample size of research projects, such as this, that examine spatially extensive populations are often limited by both cost and feasibility, which in turn limits their statistical power (Steinberg and Kareiva 1997 and Wiens 1995).

In the development of conservation strategies and management plans there is an increase in the recognition of the importance of examining the effects of change to landscape structure on connectivity. Movement is necessary at the individual level in accessing resources and at the population level in colonizing and recolonizing populations and is thus essential to population persistence. *A. maculatum* is an ideal species for examining the role of movement in mediating the effects of changes in landscape structure on populations of amphibians and ultimately on their persistence.

I have identified the importance of connectivity both at a local and broad spatial scale in population persistence of *A. maculatum* and determined at a threshold amount of suitable habitat and this thesis identifies the key elements of landscape structure and the spatial extent of *A. maculatum* populations.

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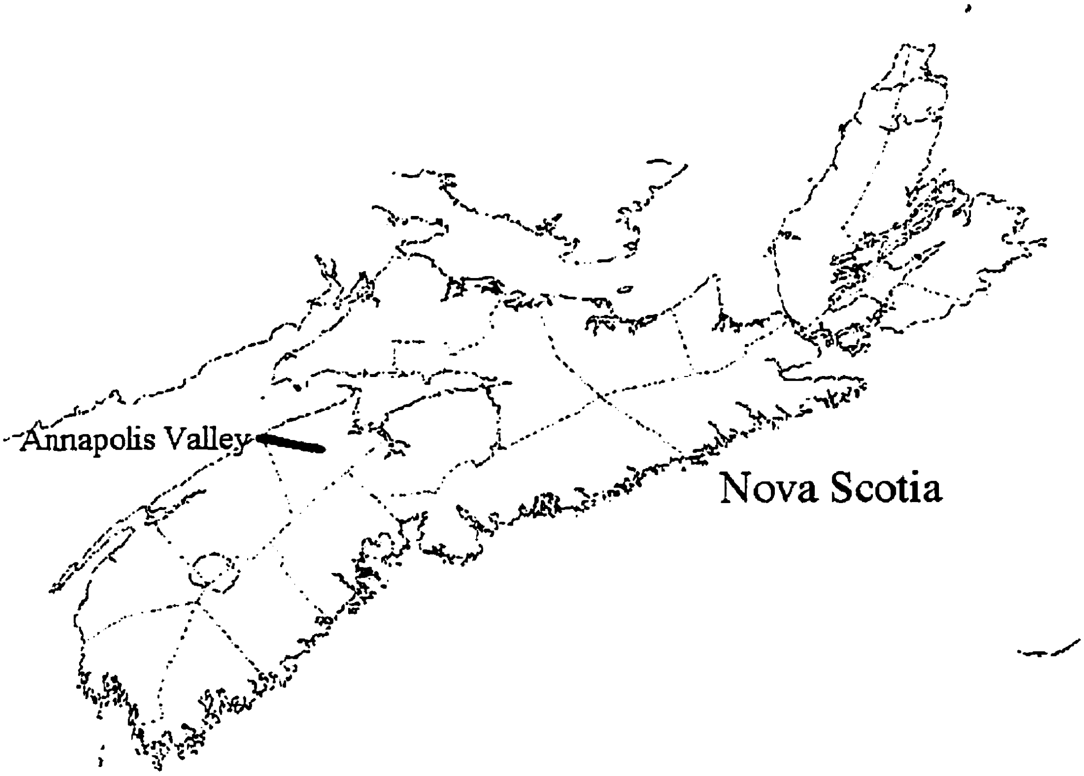
Appendix 1

Map of Nova Scotia, with the Annapolis Valley region indicated. The Annapolis Valley was the area where all ponds surveyed were located.



Appendix 2

Please note: All other data associated with these studies will be archived in the laboratory of Dr. Phil Taylor, Biology Department, Acadia University, Wolfville, Nova Scotia.

Table of UTM coordinates for ponds surveyed in Chapter 1.

Pond	Easting	Northing	*A. maculatum*
1	388275	5003600	No
2	391750	5004600	No
3	392900	5004450	No
4	392700	5004400	No
5	393050	5004375	No
6	388650	5003500	No
7	390175	5002550	Yes
8	390525	5002900	Yes
9	391850	5004125	Yes
10	388950	5005000	Yes
11	389300	5005525	Yes
12	389550	5004900	Yes
13	389100	5004000	Yes
14	389050	5004150	Yes
15	389450	5004300	Yes
16	388100	5003050	Yes

Appendix 3

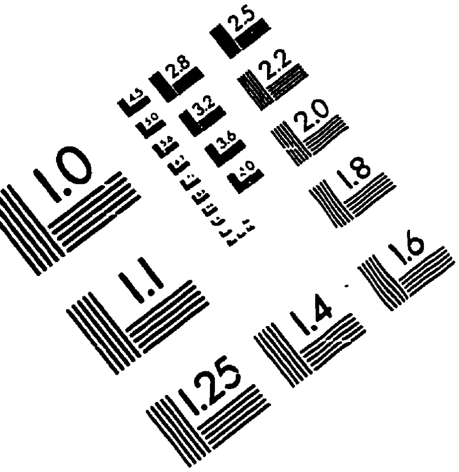
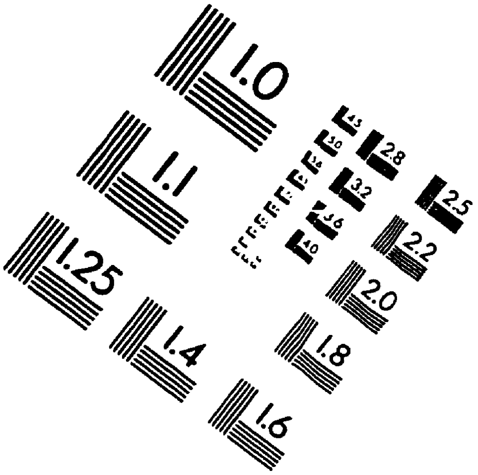
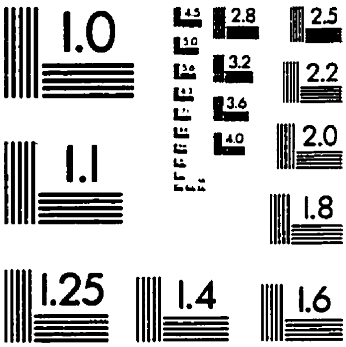
Please note: All other data associated with these studies will be archived in the laboratory of Dr. Phil Taylor, Biology Department, Acadia University, Wolfville, Nova Scotia.

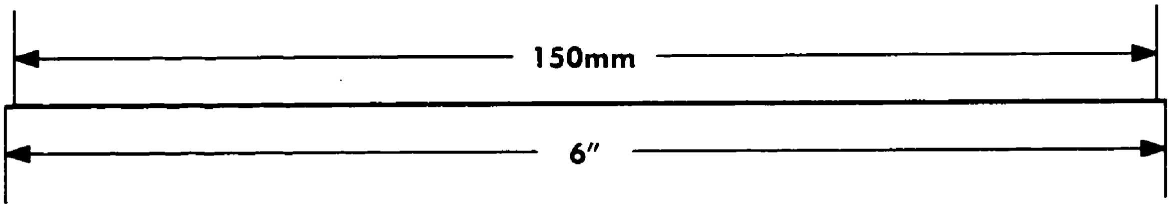
Table of UTM coordinates for ponds surveyed in Chapter 2.

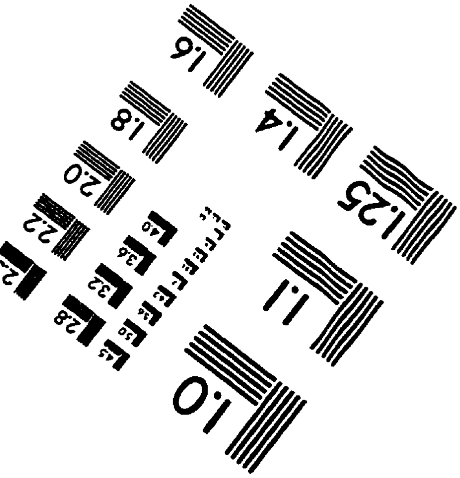
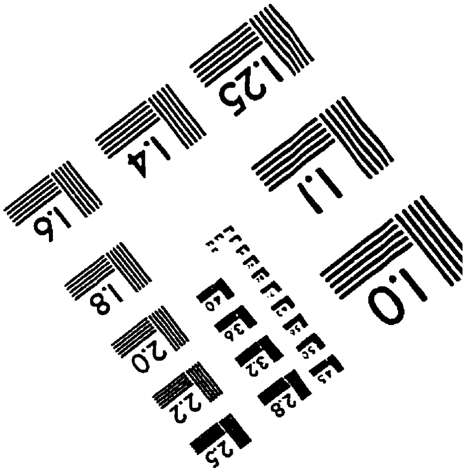
Pond	Easting	Northing	*A. maculatum*
1	375500	4997350	No
2	375250	4998750	No
3	376500	5000450	No
4	371700	4996700	No
5	367150	4992000	No
6	371200	4994400	No
7	373700	4994900	No
8	374750	4993800	No
9	380800	4995900	No
10	382550	4996850	No
11	391550	4996100	No
12	389150	4995200	No
13	390050	4996800	No
14	390400	4998850	No
15	387800	4998250	No
16	384550	4997250	No
17	382450	5001000	No
18	383500	5003025	No
19	385250	5003250	No
20	386000	5000975	No
21	388200	4989500	No
22	385200	4988250	No
23	381700	4986475	No
24	380050	4988050	No
25	377275	4996300	Yes
26	379025	4986400	Yes
27	383100	4985100	Yes
28	383500	4986550	Yes
29	392700	5001700	Yes
30	390600	5001250	Yes
31	355900	4989300	Yes
32	353600	4991250	Yes
33	358000	4990150	Yes

Pond	Easting	Northing	*A. maculatum*
34	359300	4990750	Yes
35	357550	4986250	Yes
36	359250	4984450	Yes
37	361100	4985750	Yes
38	360550	4987650	Yes
39	363400	4987050	Yes
40	365600	4985025	Yes
41	367975	4986250	Yes
42	367700	4989950	Yes
43	361600	4991875	Yes
44	363475	4992650	Yes
45	364950	4993850	Yes
46	365025	4995600	Yes
47	363400	4990925	Yes
48	369525	4987000	Yes
49	370050	4988400	Yes
50	375950	4988700	Yes
51	371500	4988850	Yes
52	377850	4988775	Yes
53	387300	4996100	Yes
54	383200	4995100	Yes
55	384500	4993600	Yes
56	379800	4999150	Yes

IMAGE EVALUATION TEST TARGET (QA-3)



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