TERRESTRIAL PACIFIC GIANT SALAMANDERS (*DICAMPTODON TENEBROSUS* GOOD) – NATURAL HISTORY AND THEIR RESPONSE TO FOREST PRACTICES

by

BARBARA JOHNSTON

B.Sc., Guelph University, 1994

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES

(Department of Zoology)

We accept this thesis as conforming

to the required standard

UNIVERSITY OF BRITISH COLUMBIA

JULY 1998

Department of Zoology

The University of British Columbia
Vancouver, Canada

Date July 24, 1998

ABSTRACT

The Pacific Giant Salamander (*Dicamptodon tenebrosus* Good) is red listed, or considered endangered, in British Columbia. Habitat loss through forest harvesting poses the largest potential threat to the species' persistence in the province. Although studies have examined the ecology of larval Pacific Giant Salamanders, virtually nothing is known about the terrestrial phase of this species: their natural history, the effects of timber harvesting, or the efficacy of proposed management strategies.

During the summer and fall of 1996 and 1997, I used radio-telemetry to examine the movements and habitat use of terrestrial Pacific Giant Salamanders in forested habitat in south-western British Columbia and north-western Washington. By tracking animals in old growth, second growth, clearcut and buffered habitats, I also investigated the effects of clearcut logging on these animals, the efficacy of riparian buffer strips for their conservation, and their dispersal or recolonization ability.

Terrestrial Pacific Giant Salamanders were found to be relatively sedentary creatures that spent the vast majority of their time in refugia such as burrows, rotten logs and streams. During the summer and fall, they wandered somewhat randomly throughout suitable habitat, showing no evidence of restricted home ranges or seasonal migrations. They were predominantly nocturnal, and their activity level was strongly associated with rain. The location of daytime refugia was associated with the availability of coarse woody debris, water, rock and leaf litter.

Although the response of terrestrial PGS to forest practices was ambiguous, some study results suggested that terrestrial Pacific Giant Salamanders may be adversely affected by clearcut logging. Catch per unit effort was lower in clearcut habitat than in forested habitat, and animals inhabiting clearcuts appeared to adjust their behaviour in ways that reduced their risk of desiccation. Riparian buffer strips twenty to thirty meters in width appeared to be a promising management strategy for the conservation of terrestrial Pacific Giant Salamanders. Buffers seemed to maintain the relative abundance of terrestrial animals at levels comparable to those in forested habitat, and the movement patterns of animals in buffer strips were indistinguishable from those of animals found in continuous forest.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Acknowledgments

I would like to thank everyone who gave me support throughout the course of this project. Many, many thanks to my supervisor Dr. William Neill for his faith and unwavering positive attitude, and to my committee members Dr. John Richardson and Dr. Anthony Sinclair for lending their ear and their advice along the way. I would also like to thank Don Utzinger and the Forest Service at Sedro Wooley for introducing me to the Nooksack River valley, and the Cultus Lake DFO lab for allowing me to use their facilities. Thanks also to Forest Renewal B.C, the B.C. Habitat Conservation Trust Fund and the Endangered Species Recovery Fund of World Wildlife Fund Canada for their financial support.

A special thanks to Angela Stringer for sharing her experiences and for her surgical help, and to my undauntable field assistants Leonardo Frid, Mark Krause, Diane Casimir, Jamie and Joy Johnston and all the others who came out for nights of salamander hunting. Thanks also to Mark Porter and Dan Haydon for their statistical help, and to the gang in the huts for understanding!

CHAPTER I

GENERAL INTRODUCTION

In recent years there has been growing concern over declines in amphibian populations world-wide (Phillips 1990, Pechmann *et al.* 1991, Blaustein and Wake 1995). Habitat loss and fragmentation are among the leading causes of this trend (Blaustein *et al.* 1994, Blaustein and Wake 1995). Amphibians have a low tolerance for environmental changes, particularly changes in moisture and temperature. These physiological constraints, along with their poor dispersal ability, make amphibians particularly vulnerable to habitat alteration (Blaustein *et al.* 1994). In British Columbia the main cause of habitat alteration is logging. Several wildlife species have been identified that are believed to be threatened by the current logging practices in the province (pending *Managing Identified Wildlife Guidebooks*, B.C. Ministry of Environment and B.C. Ministry of Forests). Among the species of concern in British Columbia is North America's largest salamander, the Pacific Giant Salamander (*Dicamptodon tenebrosus* Good, 1989).

The Pacific Giant Salamander (PGS) is a large (up to 351 mm in total length) salamander found in forested areas in the Pacific Northwest (Nussbaum *et al.* 1983). Its range extends from northwestern California, through the Cascade mountains and the Coast Range, into southwestern British Columbia (Blaustein *et al.* 1995). It is generally considered to be an obligate associate of old-growth forests (Nussbaum *et al.* 1983, Leonard *et al.* 1993), most commonly found along small, fast-flowing mountain streams. The PGS is dependent upon streams for breeding and larval development. After a two to five year larval stage, a larva either transforms into a terrestrial salamander, or it remains in the stream as a neotene, retaining its aquatic characteristics. In many small streams in the Pacific Northwest, the PGS replaces salmonid fishes as the primary vertebrate predator (Murphy and Hall 1981).

While studies have been conducted on various ecological aspects of aquatic PGS (e.g. Nussbaum and Clothier 1973, Jones *et al.* 1990, Parker 1991,1994), very little is known about the terrestrial phase of this species. Terrestrial PGS are seldom seen, presumably because they are nocturnal and fossorial. In California and Oregon their diet includes land snails, terrestrial invertebrates, other amphibians (including other PGS), snakes, lizards, birds, and small mammals (Nussbaum *et al.* 1983, Blaustein *et al.* 1995). Breeding is believed to occur once or twice per year in southern populations, with individual females reproducing every second year (Nussbaum *et al.* 1983, Blaustein *et al.* 1995). Small clutches of eggs (100 - 200) are deposited in streambeds or in underground springs, where females have been reported to guard their nests against predation (Nussbaum 1969).

In Canada, the Pacific Giant Salamander is found only in the Chilliwack River drainage and a very small portion of the Fraser River drainage. Because of its limited geographical distribution and the rapid rate at which its habitat is being lost to logging and residential development in British Columbia, the PGS has been classified as "vulnerable" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and has been red-listed (considered threatened or endangered) by the B.C. Ministry of Environment, Lands and Parks (B.C. Ministry of Environment, Lands and Parks 1993). Despite its recognition as a species at risk in B.C., very little has been done to ensure the persistence of the PGS. Only a few small sections of potential PGS habitat are protected in park lands, while the remainder of the salamander's range in B.C. is either on Crown land that is managed for timber harvesting or on private land that is undergoing residential development. In addition, small headwater streams that do not contain fish populations (S5 and S6) receive little protection from timber harvesting in British Columbia (B.C. Ministry of Environment and B.C. Ministry of Forests 1995). These streams are believed to be vital habitat for the PGS (Farr 1985).

Previous studies indicate that forest harvesting negatively affects many amphibian species (Bury 1983, Enge and Marion 1986, Pough *et al.* 1987, Ash 1988, Connor *et al.*1988, Corn and Bury 1989, Petranka *et al.* 1993, Dupuis *et al.* 1995, Vesely 1996). Some possible causes for the decline in amphibian populations following harvest include direct mortality during logging operations, increased physiological stress caused by canopy removal, disruption of stream flow, increased water temperatures, and increased stream sedimentation. For the Pacific Giant Salamander, reductions in larval densities have been reported following timber harvest (Hall *et al.* 1978, Murphy and Hall 1981, Connor *et al.* 1988, Corn and Bury 1989). Although several studies indicate that logging detrimentally affects other terrestrial amphibians (Bury 1983, Pough *et al.* 1987, Petranka *et al.* 1993, Dupuis *et al.* 1995, Vesely 1996), the effect of forest harvesting on terrestrial PGS has not yet been determined.

Under the assumption that timber harvesting negatively impacts PGS, forested riparian buffer strips have been recommended as a mitigative measure to ensure the persistence of this species in British Columbia (Farr 1985, Haycock 1991). Buffer strips effectively reduce many of the impacts of forest harvesting on stream systems by maintaining water quality, providing shade and reducing sedimentation (Newbold *et al.*

1980, Murphy *et al.* 1986, Beschta *et al.* 1987, Budd *et al.* 1987, Hartman *et al.* 1987). The few studies conducted to determine the efficacy of riparian buffer strips for the conservation of amphibians suggest that this is a useful management strategy for some species (Steventon *et al.* 1996, Vesely 1996). The utility of buffer strips for maintaining populations of terrestrial PGS has not yet been determined.

To effectively address concerns about a species at risk, such as the Pacific Giant Salamander, several things are essential. Basic natural history information about the species is required in order to identify potential threats or causes of population decline. To assess the severity of the situation, it is then necessary to determine the impacts of the potential threats on the species. Finally, before any mitigative measures are introduced, the response of the species to these measures should be determined. The objectives of this study were 1) to fill in some gaps in the natural history knowledge of terrestrial Pacific Giant Salamanders, specifically with respect to their habitat use, movements, and activity patterns; 2) to determine the effects of clearcut logging on the movement patterns of terrestrial PGS and their use of habitat, and determine the extent to which clearcut-forest edges act as barriers to potential inter-stream movements; and 3) to assess the efficacy of riparian buffer strips in maintaining populations of terrestrial PGS in the face of clearcut logging.

CHAPTER II

MOVEMENT PATTERNS AND HABITAT USE OF THE TERRESTRIAL PACIFIC GIANT SALAMANDER (*DICAMPTODON TENEBROSUS*)

INTRODUCTION

Several studies have examined the population structure, habitat use, and feeding ecology of larval Pacific Giant Salamanders (e.g. Nussbaum and Clothier 1973, Parker 1991, 1994, Kelsey 1995). Aside from the occasional anecdote reporting a fight between a terrestrial PGS and a snake (Diller 1907, Graf 1949), the discovery of a PGS nest with an attendant terrestrial adult (Henry and Twitty 1940, Nussbaum 1969), the observation of metamorphosis in captive animals (Kessel and Kessel 1944), and a proposed life history constructed from the information found in these reports (Nussbaum and Clothier 1973), essentially nothing has been published about the terrestrial stage of this species. In fact, as recently as 1985 there were no confirmed reports of terrestrial PGS in Canada (Farr 1985). Several features of their life history make these animals particularly difficult to study . They are cryptically coloured, with dark brown mottling on a lighter brown background. They are believed to spend most of their lives hidden in inaccessible retreats underground and only rarely move about on the forest floor, presumably only at night (Nussbaum *et al.* 1983, Blaustein *et al.* 1995). In addition, the fossorial and relatively sedentary nature of these animals makes them particularly difficult to locate and capture, rendering mark-recapture techniques ineffective.

Almost nothing is known about the movements or habitat use of terrestrial PGS. While most terrestrial members of the family Ambystomatidae (the family most closely related to the giant salamander family Dicamptodontidae) migrate to water in order to breed, it is not known whether terrestrial PGS undertake any sort of seasonal migration. Locations of the few documented PGS nests suggest that nesting may be restricted to subterranean springs and small headwater streams (Dethlefsen 1948, Nussbaum 1969, Jones *et al.* 1990). Terrestrial PGS are presumed to inhabit moist forested areas close to these potential breeding sites. The lack of information about terrestrial PGS leaves a significant gap in knowledge of the life history of this species. This gap is critical for conservation efforts, since the larval stage accounts for only the first two to five years of life, while individuals of this species likely live for twenty years or more (Duellman and Trueb 1986).

To learn about the secretive lives of terrestrial PGS, a means of observing or tracking these animals was required. By fitting each study animal with a radio transmitter, I was able to locate individual radio-tagged salamanders and follow their movements. Radio telemetry enabled me to address the first of this study's objectives: to fill in gaps in the natural history knowledge of terrestrial Pacific Giant Salamanders, specifically with respect to habitat use, movements, and activity patterns.

METHODS

Study Site

I conducted this study during the summer and fall seasons of 1996 and 1997 in the Chilliwack and the neighbouring Nooksack River drainage basins in southwestern British Columbia and northwestern Washington. This area falls within the Coastal Western Hemlock (CWH) biogeoclimatic zone (*sensu* Krajina 1965), with Douglas fir

(*Pseudotsuga menziesii*), Western hemlock (*Tsuga heterophylla*) and Western redcedar (*Thuja plicata*) comprising the main old-growth tree species, and salmonberry (*Rubus spectabilis*), devil's club (*Oplopanax horridus*) and sword fern (*Polystichum munitum*) dominating the understorey. The Nooksack and Chilliwack study areas are separated by approximately 20 km (straight-line distance) over a mountainous ridge. The climatic conditions in the two study areas are very similar, with a mean annual precipitation of approximately 112 cm at the Nooksack site and 144 cm at the Chilliwack site, and average annual daily maximum and minimum temperatures of 14.0 C and 5.4 C, and 13.8 C and 4.9 C respectively (National Climate Data Centre, Environment Canada). I used a total of seven study sites: two old growth (Glacier and Canyon), two second growth (Promontory and Vedder), one clearcut to the stream margin (Welcome) and two clearcut with a forested riparian buffer strip retained on either side of the stream (averaging 20 m and 30 m in width) (Dry and Gallop). Each study site was located well below an elevation of 1150 m (the highest known account of PGS in B.C.) and contained a small stream (1 m to 6 m in width) inhabited by a population of larval Pacific Giant Salamanders. Physical characteristics of each site are summarised in Table 2.1.

Capture, Radio Tagging and Release

During the first two months (mid May to mid July) of each field season, an assistant and I conducted night searches daily in order to capture terrestrial PGS. This entailed manually searching the streambed and approximately 10 m into the adjacent forest (only about 5 m at clearcut sites) with high-powered flashlights and capturing salamanders by hand or using a small net. I measured every salamander encountered (total length and snout-vent length) and weighed each to the nearest 0.1 g using an Acculab V-200 electronic scale. I immediately released animals with mass less than 25 g and retained the rest for radio implantation.

I anaesthetised the salamanders by immersion in a 0.6% solution of buffered MS-222 (tricaine methanesulfonate) and surgically implanted a small radio transmitter (Holohil model BD-2GH, mass=1.8 g, 15 x 9 x 4 mm, battery life of three to four months) into the peritoneal cavity. In 1997, I photographed the cloaca of each animal for sexing purposes and removed one toe (left hind) for ageing purposes (using the skeletochronology method). The toes were sent to Gary Matson's Laboratory (Box 308, Milltown MT 59851) to be cross-sectioned and mounted. The salamanders were held in an artificial stream channel at the Cultus Lake laboratory of the Department of Fisheries and Oceans for up to three weeks while their incisions healed. Upon recovery, I released the salamanders at the stream from which they were taken. A total of 20 salamanders, ranging in size from 29 g to 114 g, were used in this study: five from old growth habitat, six from second growth habitat, seven from riparian buffers and two from clearcut habitat. In 1996, I released each animal at the exact location where it had been captured. In 1997, I released all radio-tagged salamanders as close to their capture sites as possible, but at a standardised distance from the stream (25 m). This standard distance was approximately the average distance from the stream to the forest/clearcut interface at the buffered sites. At the two buffer sites, the salamanders were released at the actual forest/clearcut interface. These release locations were selected to determine the salamanders' response to the forest/clearcut interface at the buffered sites, and to standardise the release protocol across the remaining sites (see Chapter III).

Radio Tracking

The radio transmitters used in this study had a range of roughly 40 m to 60 m (terrain dependent). Using a hand-held directional antenna, I could determine salamander locations to an accuracy of approximately 10 cm. I recorded the location of each radio-tagged individual every second day. For each location, I recorded a description of the refuge used (refuge types: under litter, under rock, under log, in log (with log decay class), in tree roots, in ferns, on surface, in stream, other) and I left a flag marking the site. I considered an animal to have moved if its location shifted by more than 1 m from its previously recorded position. In 1996, tracking was terminated on October 30th, at which time none of the salamanders had moved for over two weeks. In 1997, I continued tracking until November 10th. At this time the batteries in most transmitters had died. Two of the animals with functional transmitters had not moved in over two weeks, while the other three remained active.

To determine diurnal activity pattern, I conducted 24 hour monitoring sessions at one site in 1996. On five occasions, the location of each salamander (n = 4) was recorded every three hours for a 24 hour period. In order to increase my sample size, in 1997 I estimated diurnal activity more coarsely on five occasions at each of five sites. During each monitoring session, I located the salamanders at dusk, at dawn the following morning, and again at dusk that evening. This method provided movement distances for one nighttime and one daytime period per session.

Climate

For the 1996 field season, I calculated air temperature and precipitation values from meteorological data collected at the Chilliwack Hatchery, located at an elevation of 240 m about 7 km from the Promontory site (elevation ~ 600 m) and 21 km from the Vedder site (elevation ~ 300 m). I calculated corrected values based on a cross-calibration using precipitation and air temperature data recorded at each study site in September and October of that year. In 1997, I installed a small weather station at each study site. Each weather station consisted of a rain gauge and two temperature data loggers (one sitting on the forest floor and one buried 20 cm below the surface).

Macrohabitat

To determine macrohabitat use, I examined the movement of the salamanders relative to the location of the stream. For every salamander location, I calculated distance to the stream and classified each location as either within the near-stream habitat (within 5 m of the water's edge) or in upslope habitat (greater than 5 m from the water's edge).

Microhabitat

At the end of each field season, I used a random number generator to select 10 telemetry locations (microsites) for each animal. For each of these "use" microsites I created a paired "non-use" microsite that was centred at a random distance (from 1 m to 20 m) and bearing from the use microsite (each determined using a random number generator). I quantified various microhabitat features associated with each microsite using a 1 m x 1 m quadrat centred at the salamander's recorded location. The features I measured included litter depth, soil depth, canopy closure, percentage ground cover (all green vegetation, shrubs, forbs, ferns, moss, leaf litter, rocks, water), number and diameter of proximate rocks, and volume and decay class of proximate large woody debris. I used a soil corer to measure the depth of organic litter (to the depth where individual leaf parts were no longer visible) and soil (from below the litter to the rock layer) at the exact salamander location. I calculated the percent total canopy closure as the average of four densiometer readings taken while standing on the exact salamander location and turning 90 degrees between readings. For ground cover measures, I estimated the percentage of the quadrat covered by each substrate type. In each quadrat, I counted the number of rocks with a diameter greater than 15 cm, recorded the diameter of each rock, and calculated the total rock diameter for the quadrat. In each quadrat, I also measured the length and diameter of all woody debris greater than 8 cm in diameter, and calculated the total volume in each decay class. I categorised woody debris according to the wood decay classes described in Bartels *et al.* (1985), in which decay class one represents intact, newly fallen wood and decay class five represents soft, broken up wood in the final stages of decay.

Data Analysis

For the analyses in this chapter I used data collected for animals at all of the forested sites (old growth, second growth and buffer). I omitted data collected at the clearcut site because this habitat type appears to affect the behaviour of terrestrial PGS (see Chapter III). I used both minimum convex polygon (MCP) and 95% adaptive kernel (AK) home range estimators to determine the approximate home range size for each salamander (CALHOME 1994). The MCP method simply connects the outermost locations obtained for each animal, and calculates the area enclosed by these locations. This method is severely affected by outliers and often either overestimates home range size by including large areas never used by the animal, or underestimates home range size because animals tend to use areas beyond those of the farthest sampled locations (MacDonald *et al.* 1980). Despite its shortcomings, I used this home range estimator because it is the most frequently used, and therefore the best for comparing home range sizes between studies. The AK method calculates the smallest area that contains a specified percentage (i.e. 95%) of the bivariate probability distribution. It thereby provides a more realistic estimate of an animal's home range size (Worton 1989).

I used basic descriptive statistics to outline the general movement and activity patterns of the salamanders radio tracked during this study. For seasonal comparisons, I divided each tracking period into summer and fall seasons, based upon the temperature and precipitation pattern recorded that year (i.e., fall was considered to begin when minimum daily temperatures dropped below 10 C and consistent rain began). In 1996, I considered the summer season to end on August 29th (and fall to begin on August 30th) and in 1997 summer ended on September 12th. Wilcoxon signed ranks tests were used to compare the mean movement length and the mean refuge duration recorded during summer and fall seasons. To determine if seasonal migrations occurred either up and downstream, or towards and away from the stream, I used Wilcoxon signed ranks tests to compare the proportion of movements made in each direction during the summer to the proportions calculated for the fall. A Wilcoxon signed ranks test was also used to compare lengths of diurnal and nocturnal movements. To determine the effect of salamander size on activity pattern, I used linear regression analyses of salamander mass versus each of the movement variables mentioned above (e.g. home range size, refuge duration, proportion nocturnal movements). Data were transformed (using log, arcsine square root and reciprocal transformations) to meet the assumptions of normality and equality of variances.

I used a series of logistic regression analyses to investigate the effects of precipitation and temperature on the activity of terrestrial PGS. The first analysis was conducted to determine if there was an association between movement (yes or no) and amount of rain that had fallen in the preceding 48 hours. A continuous salamander size variable (mass) and an interaction (mass-precipitation) variable were then added to the model to determine if the effect of precipitation on salamander movement was influenced by animal size. To assess the effects of temperature on salamander movement, separate logistic regression analyses were performed using movement (yes or no) and each temperature variable measured for the preceding 48 hour period (mean, minimum and maximum temperature). Precipitation (yes or no) and precipitation-temperature interaction variables were then added to each model to see if an interaction between precipitation and air temperature was associated with salamanders' movements. Studies on other amphibians have reported that temperature becomes a more important determinant of activity in period of low rainfall (Packer 1960, Healy 1975). Logistic regression analyses were therefore performed on each of the temperature measures (mean, minimum and maximum) and movement for those days on which no precipitation had been recorded. Once again, a continuous salamander size variable (mass) and an interaction (mass-temperature) variable were added to each model to determine if the effects of temperature on movement were associated with animal size. I examined scatterplots of salamander movement versus temperature variables to determine if there were any obvious temperature thresholds for salamander activity.

To investigate the types of refugia used by salamanders, I calculated the proportional use of each refuge type during the 1997 field season. For coarse woody debris, I also calculated the proportional use of "old" (decay classes four and five) and "new" (decay classes one to three) wood. I used a Wilcoxon signed ranks test to compare the proportional use of old and new wood to its availability at each site. Availability was calculated from the total length of woody debris in each decay class found in four 3 m radius plots at each study site (Figure 2.1).

To investigate the association of terrestrial PGS with microhabitat attributes, I performed a logistic regression analysis using data recorded at "use" and "non-use" microsites. A logistic model was used because the dependent variable was dichotomous (i.e. use or non-use site) and several of the 16 microhabitat variables measured were not distributed normally. The microhabitat variables used in this analysis are described in Table 2.2. In order to reduce collinearity between variables, those variables that were correlated with one or more other variables (Spearman rank correlation coefficients, $|r_S| > 0.7$)(Tabachnick and Fidell 1996) and those that did not differ significantly between use and non-use microsites in two-sample tests (Wilcoxon signed ranks test, $P > 0.005$) were excluded from entry into the model. Because 16 two-sample tests were run (one for each microhabitat variable recorded), the probability of a type I error (assuming $\alpha = 0.05$) was $1 - (1 - 0.05)^{16} = 0.56$ (Hays 1988). To reduce this error, significance for the two-sample tests was accepted at $\alpha = 0.005$, making the maximum probability of a type I error 0.08.

The remaining microhabitat variables were used in model development. An average use and an average non-use microsite were input into the logistic regression analysis for each individual salamander (N = 18). An animal's "average" microsite consisted of the mean value for each of the microhabitat variables, calculated from the 10 microsites measured for each individual. I used step-wise logistic regression to assess which of the remaining habitat variables were the most important predictors of microsite use by terrestrial PGS. The cut point for entry into or removal from the model at each step was set at $P = 0.15$ to reduce the likelihood that important variables be excluded (Tabachnick and Fidell 1996).

With a sample size of only 18 animals, this logistic regression analysis could easily have excluded microhabitat variables important in refuge site selection. The small sample size also made it impossible to cross-validate the model (Capen *et al.* 1986). For these reasons, I repeated the microhabitat analysis using the entire data set (all 10 microsites measured for each individual salamander, for a total N = 180). This analysis began with the step-wise logistic regression analysis used to select which variables to use in model development. Seventy-five percent of the microsites were randomly selected, and this subset was used to determine important discriminating variables using stepwise logistic regression. This procedure was repeated 25 times, and the variables selected in at least 12 of the subsets were used for model development. The final model (based on all 180 sites) was then developed using a non-step-wise logistic regression procedure.

The final model was cross-validated in order to test the classification ability of the model (Diefenbach and Owen 1989, Morrison *et al.* 1992). Seventy five percent of the microsites were randomly selected and used to make parameter estimates (using logistic regression without the stepwise procedure) for the variables appearing in the full model.

The remaining 25 % of the sites were then classified (into use and non-use sites) using the model just developed. This procedure was repeated 10 times, each time using a different, randomly selected 75% of the microsites for model development, and the remaining 25% of the microsites to determine the model's correct classification rate (CCR). For the full model, and for each of the 10 submodels, the correct classification rate was compared to the naïve classification rate of 50% using Huberty's procedure (Sharma 1996). To determine the validity of using the larger data set (N = 180) for this analysis, an "individual salamander" dummy variable was added to the final model to determine if there was a significant effect of "salamander" on this model. No significant effect would suggest that, although using 10 microsite observations per salamander violates the assumption of independence in this analysis, the lack of independence was not likely to have affected the outcome. To look more closely at the microhabitat variables deemed important by the preceding analysis, I subdivided each variable into four or five categories and performed a chi-square analysis. The contingency tables were subdivided to reveal patterns of use for the individual habitat variables (Zar 1984).

RESULTS

Ageing and Sexing

Determining the age of Pacific Giant Salamanders using the skeletochronology method proved to be unreliable, possibly due to bone resorption. Cross validation of the technique using toes taken from the same larval individuals in two subsequent years showed a correct relative age classification of only one in six (17%). My attempt to sex the salamanders using cloaca photographs was also unsuccessful. No sexual dimorphism was evident in the external cloaca structure.

Movement and Activity Pattern

Radio-tracking terrestrial PGS revealed that there was a great deal of variability in the behaviour (movement and habitat use) both within animals and between individuals of this species (e.g. Figure 2.2).

Home Range

The minimum convex polygon method generally produced smaller estimates of home range area than the adaptive kernel method. The mean home range size for terrestrial PGS was estimated as 3074 m^2 (ranging from 381 m^2 to 21,600 m^2, median = 1223 m^2) using the MCP method, and 5196 m^2 (with a range of 403 m^2 to 35,321 m^2, median = 3075 m^2) when the 95 % AK method was used. The ranges defined by tracking the animals over a two to four month period did not conform to the classic concept of a restricted home range. The size of each animal's range continued to increase as new telemetry locations were added with time (e.g. Figure 2.3).

Movement Length and Frequency

The mean daily movement distance (including days on which no movement was recorded) was 2.4 m (median = 1.9 m). This number was so low in part because of the very low frequency with which the animals moved. The average refuge duration (the number of days between movements) was 4.3 ± 0.3 d (mean ± SE, median = 4.2 d), ranging from 1 to 48 days. Regression analysis indicated that animal size (mass) could not explain the variation in refuge duration found between individuals ($R^2 = 0.03$, $F_{1,16} = 0.53$, $P = 0.48$, $N = 18$). The average length of a terrestrial PGS movement (once initiated) was 10.2 ± 1.1 m (mean ± SE, median = 8.6 m). Once again, animal size could not explain the variation between individuals ($R^2 = 0.18$, $F_{1,16} = 3.92$, $P = 0.06$, positive slope, $N = 18$).

Diel Activity Pattern

Terrestrial PGS were found to be primarily nocturnal. Seventy ± 8% (mean ± SE) of the movements made by each salamander during the dawn-dusk-dawn sessions were made at night. This distribution was significantly different from 50% (one-sample t-test: $t = 2.87$, $P = 0.01$). Animal size (mass) could not explain the individual variation in proportion of nocturnal movements ($R^2 = 0.168$, $F_{1,14} = 0.44$, $P = 0.52$, $N = 16$). The 24 h monitoring sessions conducted in 1996 resulted in a total of only 12 recorded movements. This small data set suggested that the salamanders were most active in the very early morning and least active in the afternoon (Figure 2.4). The salamanders generally moved farther during their nighttime excursions than during their daytime movements ($z = -3.20$, $P < 0.001$). The average daytime movement (once initiated) was 1.2 ± 0.4 m (mean ± SE), while at night it was 9.3 ± 1.9 m. The variation between individuals in average movement length made at night versus during the day could not be explained by salamander size ($R^2 = 0.025$, $F_{1,14} = 0.38$, $P = 0.55$, $N = 16$).

Seasonal Activity Pattern

Average length of movement did not differ significantly between summer and fall ($z = -1.37$, $P = 0.18$), but refuge duration was significantly higher during the hot, dry summer (7.1 ± 1.3 d) than in the cooler, wetter fall (4.1 ± 0.4 d) ($z = -2.84$, $P < 0.005$). There was no effect of body size on the difference in mean movement length between the summer and fall ($R^2 = 0.02$, $F_{1,16} = 0.44$, $P = 0.52$, $N = 18$). Similarly, the variation between individuals in mean refuge duration could not be explained by salamander size ($R^2 = 0.004$, $F_{1,16} = 0.08$, $P = 0.78$, $N = 18$). There was no evidence of seasonal movements up and down stream ($z = -0.09$, $P = 0.93$) or toward and away from the stream ($z = -0.36$, $P = 0.72$).

Climatic Influences on Movement

Results of the precipitation logistic regression analysis indicated that precipitation was reliably associated with movement (yes or no) in PGS (Wald $X^2 = 9.99$, $P < 0.005$). The overall correct classification of movement (yes or no) was only 58.9% (10.7% yes and 93.4% no), suggesting that based on the amount of precipitation, the logistic model predicted quite well when PGS did not move, but very poorly when they did. This discrepancy can be explained simply by the overall infrequency with which PGS moved (i.e., they usually did not move regardless of environmental conditions). Adding salamander mass and an interaction variable (mass x precipitation) to this logistic model resulted in no significant model improvement ($X^2 = 2.03$, df = 2, $P > 0.25$). This suggested that the effect of precipitation on a salamander's movement was not influenced by animal size.

The effect of air temperature on salamander movement was less direct. The logistic regression analyses performed on movement (yes or no) and each of the temperature variables (mean, minimum and maximum temperature) indicated that temperature was not reliably associated with movement (mean temperature: $X^2 = 0.21$, $P = 0.65$; minimum temperature: $X^2 = 0.62$, $P = 0.43$; maximum temperature: $X^2 = 0.06$, $P = 0.81$). Adding precipitation (yes or no) and precipitation-temperature interaction variables to the minimum air temperature model, however, resulted in a significant model improvement ($X^2 = 26.335$, df = 2, $P < 0.001$). This suggested that there was an interaction effect of precipitation and air temperature on the movement of terrestrial PGS. Logistic regression analyses performed on each of the temperature measures and movement for those days on which no precipitation was recorded indicated that only minimum air temperature was reliably associated with movement (minimum $X^2 = 6.11$, $P = 0.01$; mean $X^2 = 2.52$, $P = 0.11$; maximum $X^2 = 0.74$, $P = 0.39$). From these results I inferred that on dry days, terrestrial PGS were more likely to move if the minimum (nighttime) air temperature was low than if it was high. Adding mass and mass-temperature interaction variables to the model revealed that the effect of temperature on movement was not associated with animal size (mass) (Wald $X^2 = 0.77$, $P = 0.38$). Temperatures recorded by data loggers buried 20 cm below the soil surface remained quite constant, while temperatures recorded at the forest floor fluctuated (particularly in open habitat such as clearcuts) (Figure 2.5).

Data collected during the 1996 field season suggested that terrestrial PGS may have had a minimum temperature threshold for movement at approximately 0 C (Figure 2.6). I recorded no movements on days when the minimum temperature was below 0.5 C. These results were confounded by the fact that low temperatures were recorded only late in the season, approximately when the salamanders ceased moving for the winter. In 1997, however, all of the salamanders were still active well past the date of inactivity in 1996. This challenged the idea that season (time of year), rather than temperature, triggered inactivity in the animals in 1996. In 1997, minimum daily temperatures were still above 0.5 C when the study was terminated in mid November. I found no evidence of movement thresholds in the other daily air temperature measures recorded (mean temperature and maximum temperature).

Macrohabitat Use

The influence of forest type (logging history) on the activity of terrestrial PGS will be discussed in Chapter III. There was a great deal of individual variation in the average distance salamanders were found from the stream. Some animals confined their movements to within 1 m of the stream (e.g. Figure 2.7a) while others lived almost exclusively in upslope areas (e.g. Figure 2.7b). On average, the majority of each animals' observations were made in near-stream habitat (within 5 m of the water's edge) (67.2 ± 6.9%, mean ± SE) versus in upslope habitat. Again, there was a great deal of individual variation, ranging from zero to 100%.

Microhabitat Use

Refuge Types

There was a great deal of variation in the proportional use of refuge types. In part, this was likely due to differences in availability of refugia at each site. Unfortunately it was not possible to calculate availability for a number of the refuge types (i.e., underground, on the surface). Comparison of the proportional use of refugia averaged across individuals indicated that coarse woody debris (38%), underground (likely in burrows and root channels) (31%) and rocks (26%) served as the most common places of refuge (Figure 2.8). When the salamanders were located in coarse woody debris, they were found in old wood (decay classes four and five) 91% of the time and in new wood (decay classes one to three) only 9% of the time. Based upon the availability of wood in each decay class measured at four 3-m radius plots at each study site, the proportional availability of old and new wood was approximately 50:50 (averaged across the study sites). The salamanders, therefore, used new wood significantly less than expected according to availability ($z = -3.19$, $P = 0.001$) (Figure 2.9).

Microsite Selection

After excluding variables that did not differ between use and non-use sites in pair-wise comparisons (Table 2.3), as well as correlated variables (Table 2.4), only six variables remained for entry into the stepwise logistic regression analysis (DROCK, WOOD, SDEPTH, WATER, GREEN, and LITTER). The "average" microsite stepwise analysis (using N=18 sites) revealed that three variables were significant determinants of microsite use by PGS (DROCK, WOOD, and WATER). These variables were used to create the final logistic model. The overall correct classification rate for the model was 87.7% (85% use and 90% non-use). Wald tests performed on each of the dependent variables found in the model indicated that only two of the variables (WOOD and WATER) were reliably associated with the classification (use or non-use) ($P < 0.05$) (for DROCK, $P = 0.07$).

When the analysis was repeated using the entire data set (all 10 microsites measured for each individual salamander making a total N = 180) the step-wise logistic regression analysis revealed four microhabitat variables that were significant determinants of microsite use (DROCK, WOOD, WATER and LITTER). The final model developed using these variables was the linear logistic model:

$$\theta_i = \frac{e^y}{1 + e^y}$$

where,

$$y = 0.31 - (3.7 \text{ x } 10^{-3})\text{DROCK} - (7.2 \text{ x } 10^{-6})\text{WOOD}$$

$$- (1.7 \text{ x } 10^{-2})\text{WATER} + (8.1 \text{ x } 10^{-3})\text{LITTER}.$$

Wald tests performed on each of the dependent variables found in the model indicated that all four variables were reliably associated with microsite classification (use or non-use) ($P < 0.05$). The mean CCR of the submodels did not differ significantly from the CCR of the full model for used (full = 64%, submodels = 61%, $P = 0.35$) or for non-used (full = 79%, submodels = 74%, $P = 0.13$) microsites. Huberty's procedure revealed that the CCRs of the full model ($P < 0.0001$) and of each of the submodels ($P < 0.005$) were better than expected by chance. Inputting individual salamanders as a dummy variable into the final logistic regression analysis indicated that there was no significant effect of "salamander" on this model (Wald test: X^2=0.66, P=0.42).

Chi-square analysis indicated that for each of the four habitat variables deemed to be important in microsite use (DROCK, WOOD, WATER and LITTER) there was a significant difference in category frequencies between use and non-use microsites ($P < 0.01$). Subdivision of the contingency tables revealed that PGS were found at microsites with no wood (category one) much less frequently than predicted, and at microsites with wood volume in the three highest categories (three to five) more frequently than predicted ($P < 0.05$) (Figure 2.10a). The salamanders were found less frequently than expected at microsites with no rock (category one), and more frequently than expected where there was a very high total diameter of rocks (category five) ($P < 0.05$) (Figure 2.10b). At microsites with no water (category one) PGS were found less frequently than predicted ($P < 0.001$). At microsites where water was present and covered 1% to 75% of the microsite (categories two to four), PGS were found more frequently than predicted ($P < 0.01$) (Figure 2.10c). The relationship between microsite use and leaf litter cover was less intuitive. PGS were found more frequently than expected where leaf litter covered less than 25% of the microsite (category one) ($P < 0.001$) and less frequently than expected where litter covered greater than 75% of the microsite (category five) ($P < 0.001$) (Figure 2.10d). In summary, PGS were found at microsites with more wood, more rock and more water than was generally available in their habitat.

DISCUSSION

Movement and Activity Pattern

The data I used to determine the activity patterns of terrestrial PGS were collected by following the movements of radio-tagged animals. Time constraints and the small number of salamanders captured made it impossible for me to test the effects of radio implantation on the behaviour of terrestrial PGS. In a recent study investigating the movements of radio-implanted Spotted Salamanders (*Ambystoma maculatum*), laboratory validation procedures were conducted using radio-tagged and control animals to determine the effects of radio implantation on the feeding behaviour, mass, and survival of these salamanders (Madison 1997). Results of this study suggested that there were no long-term effects of the surgeries or implantations on the salamanders. The feeding behaviour of the implanted animals was indistinguishable from that of the control animals within seven days of surgery, and the implantation procedure did not affect the mass of the salamanders. The survival rate of radio-tagged individuals in the field was comparable to annual adult survivorship values reported in previous studies conducted on this species. The Spotted Salamanders used in this study ranged in size from 14.3 g to 33.6 g, and the radio transmitters had a mass of either 2.1 g or 2.7 g (depending on the model used). Because the transmitters used in Madison's study were larger than those used in my study (1.8 g), and the salamanders he used were generally smaller (minimum mass in my study was 28.7 g), I am quite confident that the transmitter implants did not significantly affect the behaviour of the terrestrial PGS used in my study.

My observations of radio-tracked animals suggested that terrestrial PGS did not inhabit restricted home ranges. An animal's home range has traditionally been described as a defined area inhabited by the animal that provides everything required for survival and reproduction (Dice 1952). Areas utilised by the radio-tracked PGS appeared indefinite both in space and in time. The salamanders did not cover their ranges regularly. In fact, they virtually never returned to a location that they had previously occupied during the three-month tracking period. In addition, the size of each animal's range continued to increase as new telemetry locations were added over time. The classic home range asymptote, defined as the point at which the addition of more telemetry locations for that animal does not increase the estimated size of its home range (Harris *et* *al.* 1990), was never reached for the PGS tracked in this study (e.g. Figure 2.3). Figure 2.3 also illustrates why the home range size estimates made using the minimum convex polygon method were generally smaller than those made using the adaptive kernel method. While both methods underestimate home range size when the asymptote is not reached, the underestimation is usually greater using the MCP method because the size estimate increases more slowly with the addition of more observations per individual (Schoener 1981). Because the animals appeared to wander unrestricted throughout their surroundings, I concluded that the actual home range of each animal was best defined simply as the available area of suitable habitat. Similar situations of indefinite home ranges have been reported in other reptiles and amphibians (skinks *Eumeces fasciatus* and *Scincella laterale*, Fitch and von Achen 1977; mole salamanders *Ambystoma talpoideum*, Semlitsch 1981; red-spotted newts *Notophthalmus viridescens,* Harris 1981). The average home range sizes reported for other terrestrial salamander species are extremely variable, ranging from very small (e.g. 0.6 m^2 in the Otter salamander (*Plethodon hubrichti*; Kramer *et al.* 1993), and 1.4 m^2 in the Dusky salamander (*Desmognathus fuscus*; Ashton 1975) to very large and similar to terrestrial PGS (Northwestern salamander (*Ambystoma gracile*), Angela Stringer, University of Washington - pers. comm.). There are problems associated with comparing home range sizes between studies because of the different time scales over which studies have been conducted, and because of the sensitivity of most home range estimators to the number of animal locations used in calculating home range size.

As is the case with most amphibians, my study indicated that terrestrial PGS were rather sedentary creatures (Duellman and Trueb 1986, Sinsch 1990). They spent most of their time in refuges, commonly going several days (occasionally even weeks) without changing their location. Although these animals were capable of travelling long distances (the maximum distance travelled between checks was 67 m), the average movement length recorded during this study was only 10.2 m, with an average movement rate of 2.4 $m \cdot d^{-1}$. These distances seemed quite short when compared to movement distances recorded for closely related ambystomid salamanders, for which movement rates have been reported in meters travelled per hour (i.e. 13.9 $m \cdot hr^{-1}$ in adult mole salamanders (*Ambystoma talpoideum*), Semlitsch 1981; 50.8 $m \cdot hr^{-1}$ in adult California Tiger Salamanders (*Ambystoma californiense*), Loredo *et al.* 1996). The observations of ambystomid salamanders noted above were recorded during breeding migrations either to or from breeding ponds. During my study I found no evidence of a breeding migration in terrestrial PGS, at least during the summer and fall seasons for which I have data. The activity level of terrestrial PGS, therefore, would be more appropriately compared to the activity of other salamander species during the portion of the year when they are not making directional movements. Presumably because of the difficulty in capturing animals outside of breeding migrations, this information has not been collected for other terrestrial salamander species.

My results indicated that although the terrestrial PGS did move short distances during the day, they were predominantly nocturnal animals. This is the case with most terrestrial salamanders (Semlitsch 1981, Semlitsch and Pechmann 1985, Kramer *et al.* 1993), and is generally considered to be an adaptation to reduce the risk of both desiccation and predation. My results indicated that terrestrial PGS remained in their refugia longer during the summer season than during the fall. Seasonal differences in activity pattern have also been reported for several other salamander species (Ashton 1975, Healy 1975, Madison 1997). I hypothesised that this was also an adaptation to reduce the risk of desiccation during the warmer, dryer summer season. It has been proposed that since the predation risk for terrestrial salamanders by snakes and predatory birds is highest during the summer, salamanders may be more active in the spring and fall when movement is less risky (Madison 1997).

Results of this study indicated that the activity level of terrestrial PGS was dependent upon precipitation. Because amphibians have thin, highly permeable skin, evaporative water loss may become a serious problem when moving from one area to another (Sinsch 1990, Zug 1993). The risk of desiccation is greatly reduced when surface movements are conducted during the rain or shortly after rain when the ground is still moist. An association between precipitation and movement has been reported in many other amphibian species (Packer 1960, Kleeberger and Werner 1982, Semlitsch 1985, Palis 1997). Laboratory studies have shown that a species' desiccation tolerance is an evolved trait that has been selected by its natural environment (Ray 1958). The Pacific Giant Salamander is a denizen of coastal temperate rainforests, where the forest floor remains cool and moist (Nussbaum *et al.* 1983). Terrestrial PGS, therefore, would be expected to have a relatively low tolerance for desiccation, forcing them to modify their behaviour in order to minimise this risk.

My results indicated a relatively weak association between terrestrial PGS activity and air temperature. This was a bit surprising because laboratory studies conducted on thermal tolerances of various amphibian species suggested that these animals could be quite sensitive to fluctuations in air temperature (Ray 1958, Hutchinson 1961). While I found that the air temperatures recorded at the forest floor could fluctuate dramatically over a short period of time (particularly in open habitat such as clearcuts), temperatures recorded 20 cm down in the soil remained remarkably constant, fluctuating a maximum of 4 C daily (Figure 2.5). Because terrestrial PGS are almost strictly fossorial, the temperatures to which they were subject during this study remained almost constant. This may explain the salamanders' insensitivity to the temperature fluctuations that occurred above ground. A possible exception occurred in 1996 when air temperatures dropped close to the freezing point. Figure 2.6 suggested that terrestrial PGS may have had a minimum temperature threshold of approximately 0.5 C, below which they ceased moving. This was consistent with the finding of a study on Spotted Salamanders (*Ambystoma maculatum*) in which individuals froze to death if they were not able to find suitable burrow refuges before surface temperatures dropped below freezing (Madison 1997). The activity level of terrestrial PGS also appeared to be more dependent upon air temperature when the weather was dry. During periods without rainfall, I found that the salamanders were more likely to move if the air temperature was low than if it was warm. A possible explanation is that surface condensation (dew) was more likely to form on cold dry nights than on warm dry nights, making moisture conditions more favourable for salamander movements.

In this study I found that movement and activity patterns of terrestrial PGS were not dependent upon animal size. This was inconsistent with previous findings that the higher surface to volume ratio associated with small amphibians resulted in a higher risk of desiccation and a lower tolerance for thermal stresses (Ray 1958, Spotila 1972, Semlitsch 1981). This inconsistency suggested that the range of temperatures and moisture levels encountered by the salamanders during this study fell within the range of tolerance of even the smallest radio-tagged terrestrial PGS. Because I implanted radio transmitters intraperitoneally, I was restricted to using animals greater than 25 g in mass. It is possible that smaller, recently metamorphosed animals would have displayed different movement and activity patterns than the relatively large animals I used in this study.

Habitat Use

On average, the salamanders tracked during this study remained in the near-stream habitat (within 5 m of the water's edge) 67% of the time. Movements in relation to the stream were extremely variable between individuals. Some animals were always observed close to the water, while others had no recorded streamside locations (e.g. Figure 2.7). It is possible that some of the individual variability I observed in this study (i.e., the relation of salamanders to the stream) may have been explained by the sex of the animals. The activity pattern of males and females have been found to differ in some salamander species (Staub *et al.* 1995). The terrestrial PGS that I observed remaining close to the stream, for example, may have been females depositing eggs and guarding their nests against predation. Unfortunately, there was no method for determining the sex of the Pacific Giant Salamanders used in this study without sacrificing the animals.

Terrestrial PGS used coarse woody debris, underground burrows or root channels, and rocks as their most common places of refuge. Any structure that served to increase the moisture of a microsite appears to have made a suitable resting site. This was consistent with findings from studies on other terrestrial salamanders that used small mammal burrows (Maiorana 1978, Semlitsch 1981, Loredo *et al.* 1996, Madison 1997), woody debris (Wells 1980, Kleeberger and Werner 1982, Parmelee 1993, Dupuis *et al.* 1995) and rocks (Ashton 1975, Jaeger 1980a) as refugia. When the Giant Salamanders used coarse woody debris as a refuge, they appeared to have selected older wood, in advanced stages of decay over newly fallen wood. The same result was found for Western Red-backed Salamanders (*Plethodon vehiculum*) on Vancouver Island, B.C. (Dupuis 1993). Old wood is soft and therefore easy for salamanders to burrow into. It also has a higher moisture content than newly fallen wood (Triska and Cromack 1979).

Local microhabitat use by terrestrial PGS may in part have been determined by the availability of coarse woody debris, rock, water, and leaf litter. PGS were found at microsites with more wood, rock and water than was generally available in their habitat. The correct classification rate (~ 70%) associated with the microhabitat model suggested that there were other factors important to microsite selection that were not considered in this analysis. This was not surprising, given that terrestrial PGS are predominantly fossorial animals, and only surface habitat variables were used in this analysis. Furthermore, a study conducted on another terrestrial salamander species (*Plethodon glutinosus*) suggested that the spatial distribution of animals is not simply influenced by the availability of suitable microhabitats, but also by interactions among individuals (Wells 1980).

Table 2.1. Physical characteristics of each study site.

site	year studied	habitat type	stand age (years)	river valley	altitude (m)	aspect	average slope	tree composition[b]
Promontory	1996	2nd growth	70	Chilliwack	600	SSW	9°	TSHE / THPL / ACMA
Vedder	1996	2nd growth	30	Chilliwack	300	ESE	10°	TSHE / ALRU / THPL
Canyon Creek	1997	old growth	117	Nooksack	445	SSE	4°	TSHE / PSME / THPL
Glacier Creek	1997	old growth	128	Nooksack	415	WSW	11°	PSME / TSHE / THPL
Gallop Creek	1997	buffered	4[a]	Nooksack	695	NNW	11°	TSHE / ABPR / ALRU
Dry Creek	1997	buffered	4[a]	Nooksack	646	N	19°	TSHE / ALRU / THPL
Welcome Pass	1997	clearcut	9	Nooksack	677	S	14°	PSME / TSHE / THPL

[a] stand age outside of the riparian buffer zone

[b] ABPR = Noble fir (*Abies procera*), ACMA = Bigleaf maple (*Acer macrophyllum*), ALRU = Red alder (*Alnus rubra*), PSME = Douglas-fir (*Pseudotsuga menziessi*), THPL = Western redcedar (*Thuja plicata*), TSHE = Western hemlock (*Tsuga heterophylla*), listed in order of dominance

Table 2.2. Description of microhabitat variables used in the logistic regression analysis.

variable name	**variable description**
CANOPY	canopy closure
DROCK	total diameter of rocks
EXROCK	% cover of exposed rocks
#ROCKS	number of rocks
FORBS	% cover by forbs
FERNS	% cover by ferns
GREEN	% cover by all green vegetation
LITTER	% cover by leaf litter
MOSS	% cover by moss
N_WOOD	density of new woody debris (decay classes 1 to 3)
O_WOOD	density of old woody debris (decay classes 4 and 5)
LDEPTH	litter depth
SDEPTH	soil depth
SHRUBS	% cover by shrubs
WATER	% cover by water
WOOD	total density of coarse woody debris

Table 2.3. Wilcoxon signed ranks tests used to exclude microhabitat variables from the microhabitat logistic regression analysis.

variable	**z**	**P (2 tailed)**
CANOPY	-0.85	0.39*
DROCK	-4.91	<0.001
EXROCK	-4.05	<0.001
FERNS	-1.47	0.14*
FORBS	-2.17	0.03*
GREEN	-3.14	0.002
LDEPTH	-0.89	0.37*
LITTER	-6.14	<0.001
MOSS	-1.06	0.29*
N_WOOD	-1.70	0.09*
#ROCKS	-4.04	<0.001
O_WOOD	-6.25	<0.001
SDEPTH	-3.64	<0.001
SHRUBS	-3.15	0.002
WATER	-5.20	<0.001
WOOD	-6.58	<0.001

* variables with P>0.005 were excluded from entry into the microhabitat logistic regression model

Table 2.4. Spearman rank correlation matrix (r_s values) used to exclude microhabitat variables from entry into the microsite logistic regression model.

r_s	DROCK	EXROCK	GREEN	LITTER	#ROCKS	O_WOOD	SDEPTH	SHRUBS	WATER	WOOD
DROCK	1.00	0.90*	-0.16	-0.48	0.99*	-0.15	-0.37	-0.04	0.41	-0.17
EXROCK	0.90*	1.00	-0.17	-0.48	0.90*	-0.17	-0.32	-0.03	0.38	-0.19
GREEN	-0.16	-0.17	1.00	-0.06	-0.15	-0.12	0.08	0.59	-0.13	-0.11
LITTER	-0.48	-0.48	-0.06	1.00	-0.47	-0.06	0.46	-0.05	-0.55	-0.09
#ROCKS	0.99*	0.90*	-0.15	-0.47	1.00	-0.14	-0.35	-0.01	0.40	-0.16
O_WOOD	-0.15	-0.17	-0.12	-0.06	-0.14	1.00	-0.15	-0.03	0.07	0.94*
SDEPTH	-0.37	-0.32	0.08	0.46	-0.35	0.15	1.00	0.08	-0.44	-0.15
SHRUBS	-0.04	-0.03	0.59	-0.05	-0.01	-0.03	0.08	1.00	-0.03	-0.02
WATER	0.41	0.38	-0.13	-0.55	0.40	0.07	-0.44	-0.03	1.00	0.08
WOOD	-0.17	-0.19	-0.11	-0.09	-0.16	0.94*	-0.15	-0.02	0.08	1.00

* variables correlated with $|r_s| > 0.7$ were excluded from entry into the model

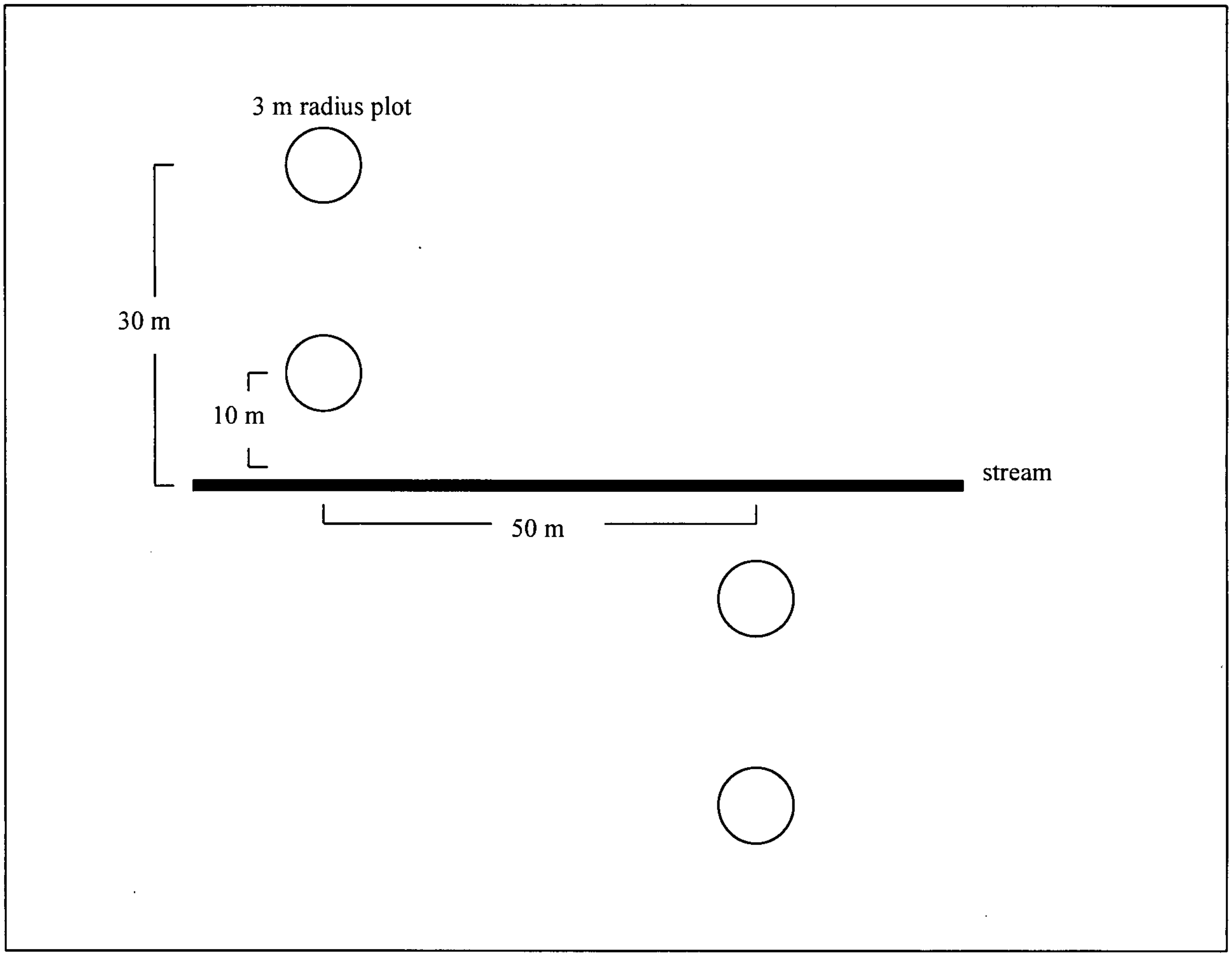

Figure 2.1. Location of 3 m radius plots used to calculate available coarse woody debris at each study site.

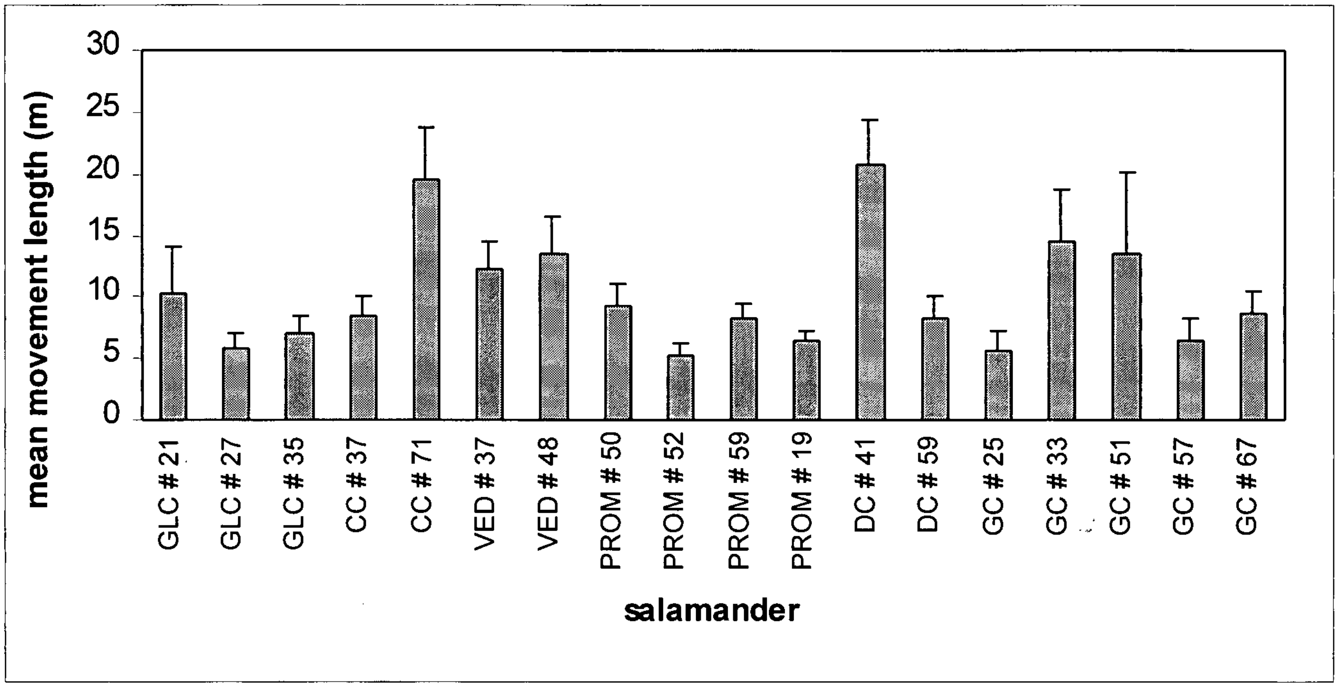

Figure 2.2. Mean length of movement (once initiated) for each salamander. Error bars are one standard error of the mean. Study site abbreviations: GLC = Glacier Creek, CC = Canyon Creek, VED = Vedder, PROM = Promontory, DC = Dry Creek, GC = Gallop Creek.

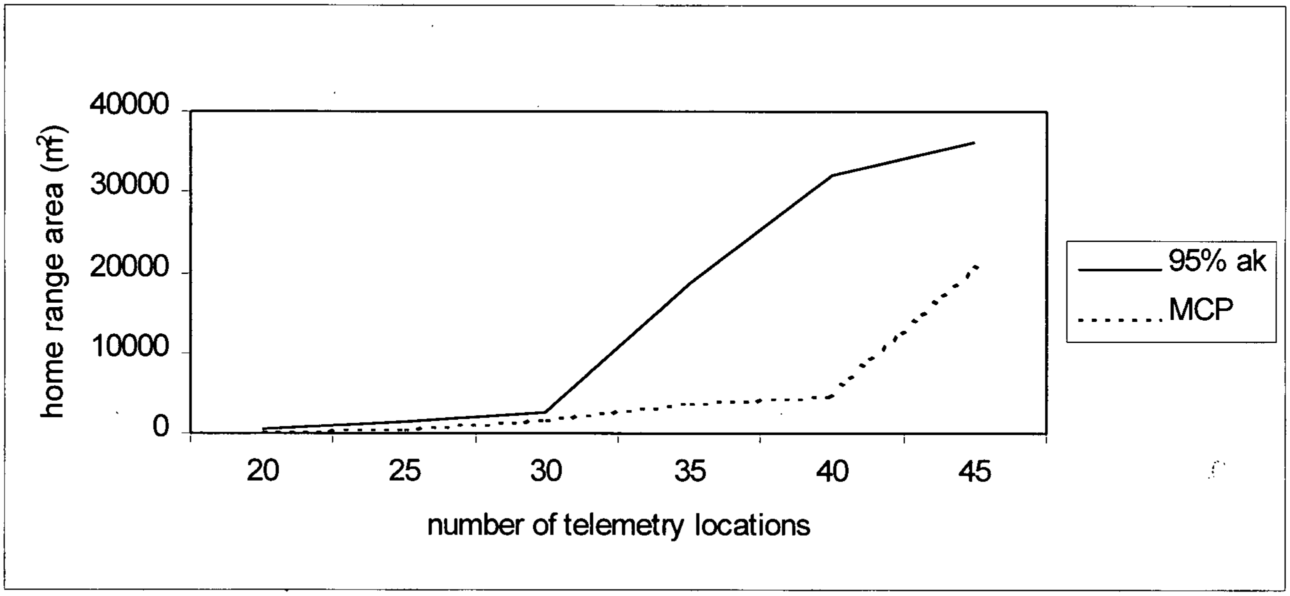

Figure 2.3. Minimum convex polygon (MCP) and 95% adaptive kernel (95% ak) estimates of home range size for an increasing number of radio telemetry locations (salamander #71 at the Canyon Creek site).

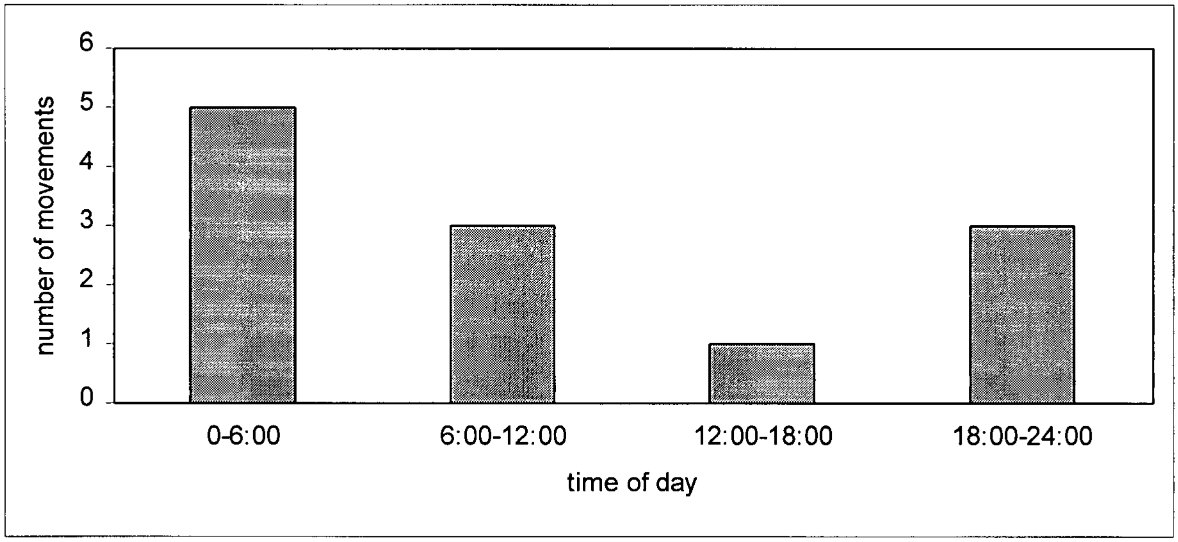

Figure 2.4. Average daily activity pattern of terrestrial Pacific Giant Salamanders determined from 24 hour monitoring sessions conducted at one site (N= 4) on five separate occasions in 1996.

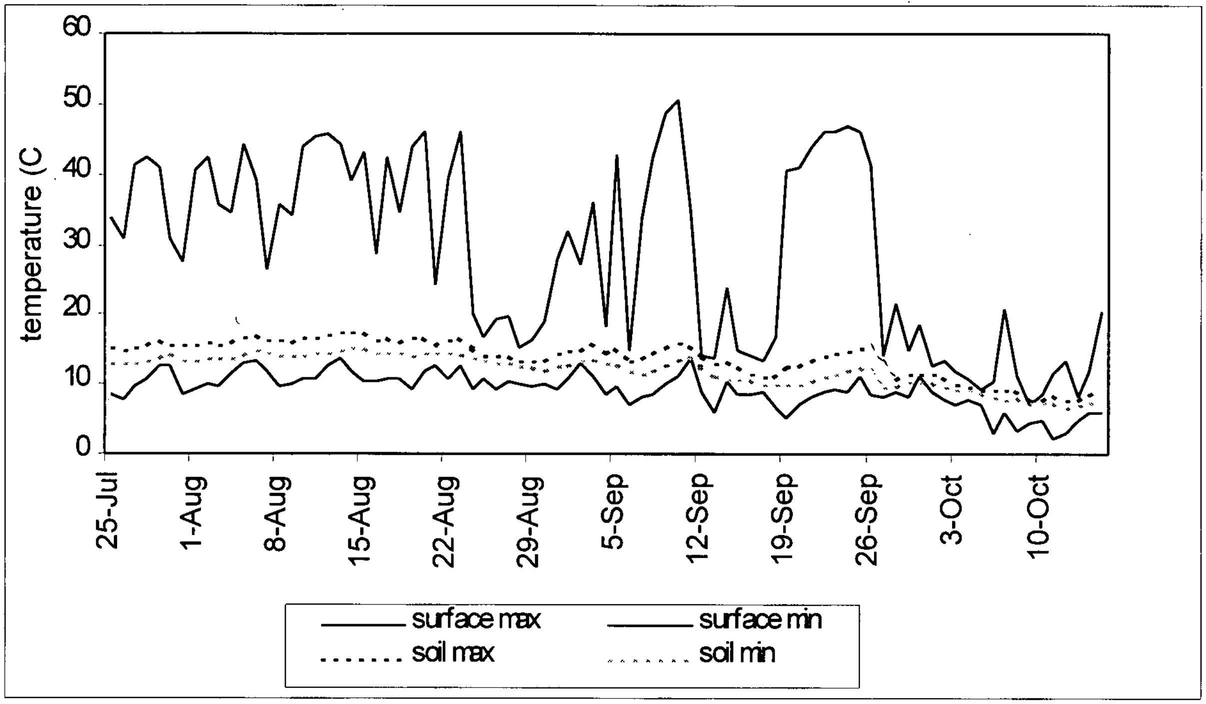

Figure 2.5. Daily maximum and minimum temperatures recorded at the forest floor (surface) and 20 cm underground (soil) at a clearcut site during the 1997 field season.

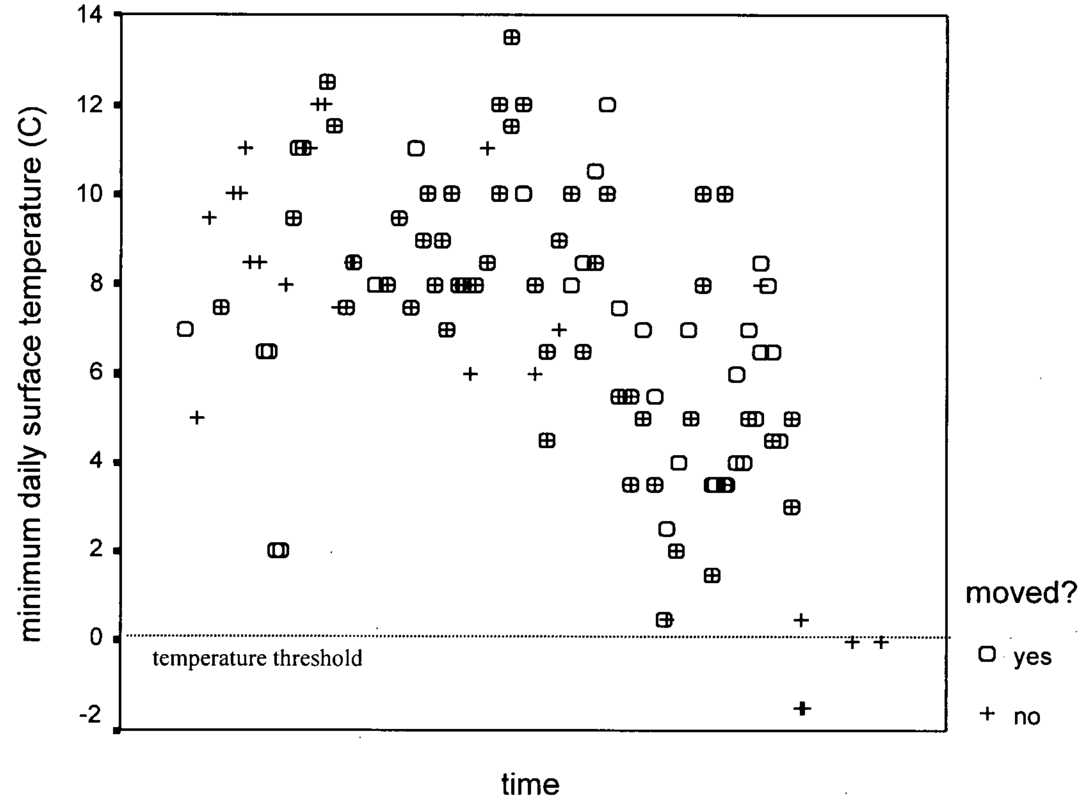

Figure 2.6. The effect of minimum surface temperature on the movements of terrestrial Pacific Giant Salamanders over time (July to November) during the 1996 field season.

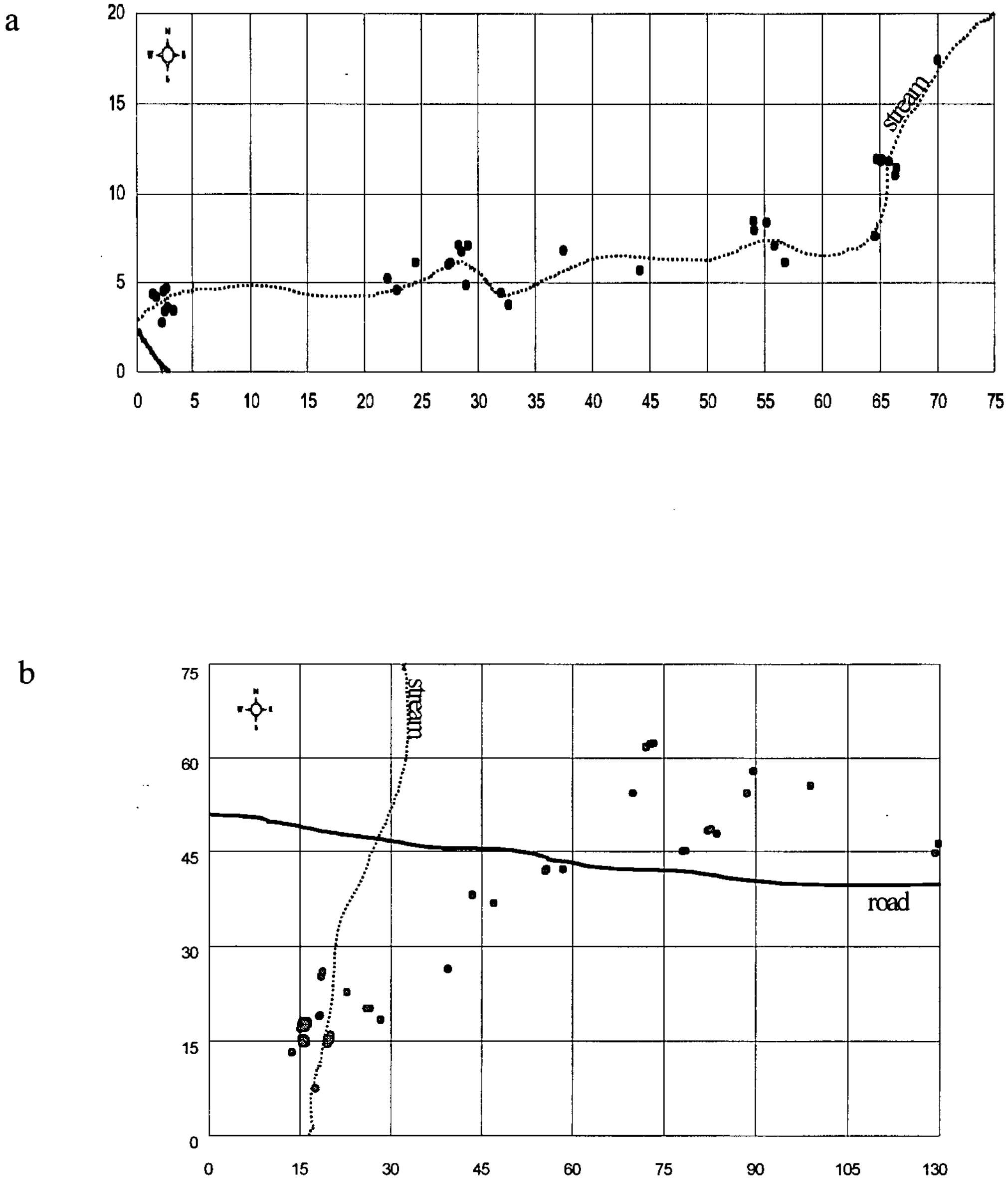

Figure 2.7. Telemetry locations for two Pacific Giant Salamanders shown on a grid measured in meters: (a) #37 from the Vedder site and (b) #50 from the Promontory site.

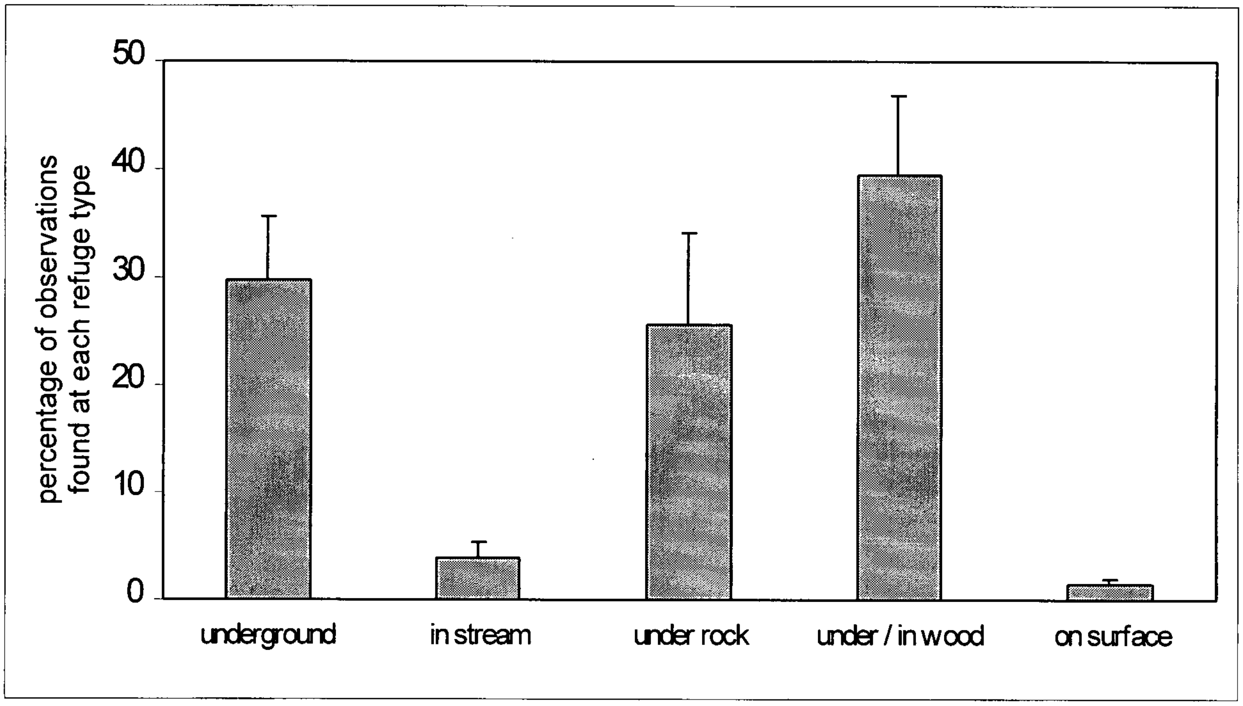

Figure 2.8. The proportional use of different refuge types by terrestrial Pacific Giant Salamanders (averaged across all individuals, N = 18). Error bars are one standard error of the mean.

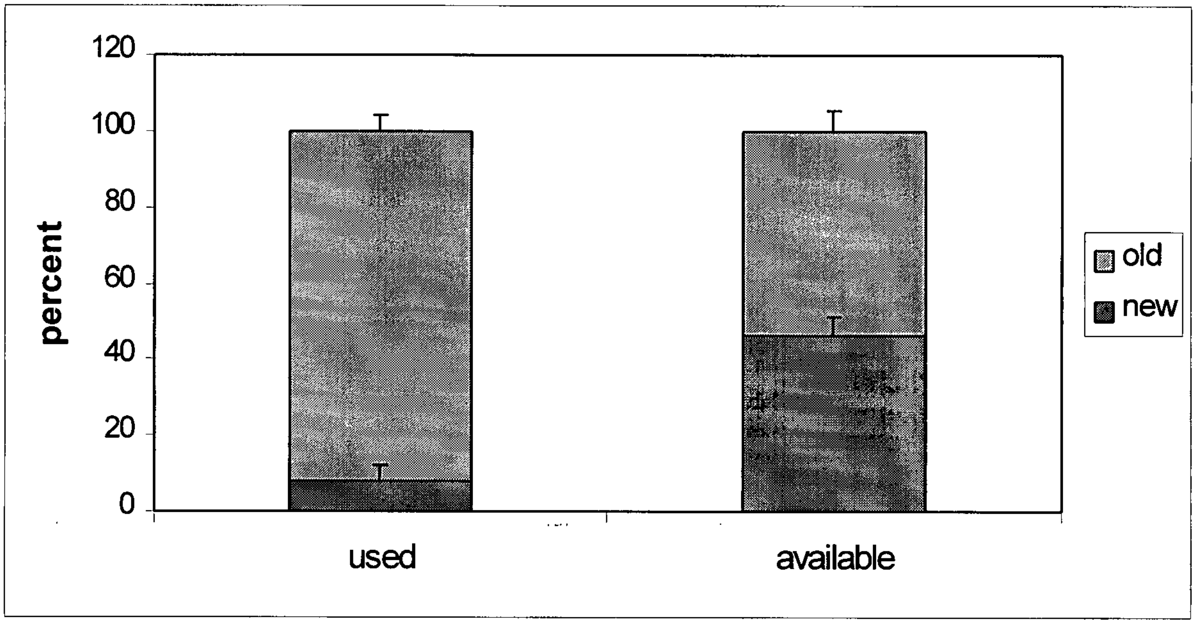

Figure 2.9. Average percent of new (decay classes one to three) and old (decay classes four and five) woody debris available and used as refugia by terrestrial Pacific Giant Salamanders. Error bars are one standard error of the mean.

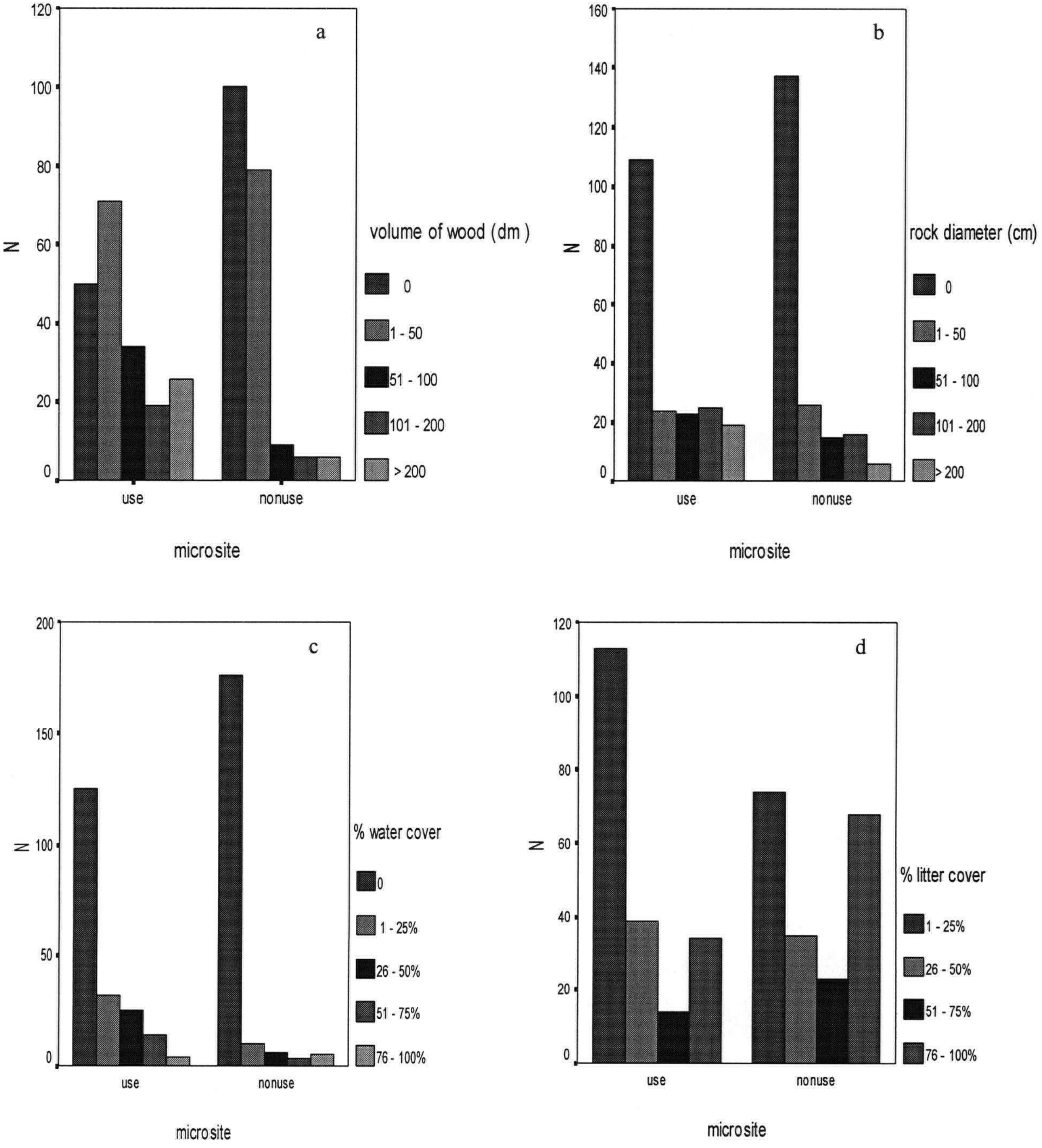

Figure 2.10. Frequency histograms showing use and availability (non-use) of (a) wood, (b) rock, (c) water and (d) leaf litter in different categories.

CHAPTER III

EFFECTS OF CLEARCUT LOGGING ON TERRESTRIAL PACIFIC GIANT SALAMANDERS (*DICAMPTODON TENEBROSUS*) AND MANAGEMENT IMPLICATIONS

INTRODUCTION

The Pacific Giant Salamander has been identified as a species at risk in British Columbia. It is designated as "vulnerable" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and has been placed on the Red List by B.C. Environment, indicating that it is "threatened or endangered" in the province (B.C. Ministry of Environment, Lands and Parks 1993). Farr (1985) and Haycock (1991) reported that the main threat to this species is the intensive forest harvesting underway in the only valley where the species persists in Canada, the Chilliwack River valley. In order to effectively manage for the conservation of the PGS, it is essential that we determine the effects of clearcutting (the predominant harvesting method used in the Chilliwack valley) on this species. Several studies focusing on the effects of clearcutting on larval PGS suggest that these animals may be adversely affected by clearcutting (Bury 1983, Conner *et al.* 1988, Corn and Bury 1989). This is likely due to an increased input of fine sediment into the stream caused by logging and associated road building. Perhaps because of the difficulties inherent in studying terrestrial PGS, no studies have been conducted to assess the impacts of clearcut logging on the terrestrial life stage.

Methods commonly used to determine the effects of habitat alteration on a species or community involve comparing population densities or relative abundance in altered and unaltered (control) areas. These methods are not effective for terrestrial PGS. The relatively sedentary and secretive nature of these animals makes them particularly difficult to find using the standard amphibian techniques (pitfall traps, time and area constrained searches). It has proven unfeasible to catch sufficient numbers of terrestrial PGS to make population comparisons (see Kelsey 1995 and Vesely 1996). In addition, the standard techniques only account for individuals occurring on the surface or hiding under small cover objects, while terrestrial PGS spend the majority of their time underground or under immovable forest structures (see Chapter II). In order to determine the effects of habitat alteration on terrestrial PGS, a method that does not involve the comparison of population sizes must be used. By radio-tracking individual terrestrial PGS I was able compare the behaviour of animals living in habitats with different harvesting histories, thereby assessing the effects of logging on certain aspects of the ecology of these animals.

The objectives of this chapter were (1) to assess the effects of clearcutting on the behaviour of terrestrial PGS, (2) to determine the efficacy of riparian buffer strips as a mitigative measure for the preservation of terrestrial PGS in the face of clearcut logging, and (3) to determine the dispersal capability of terrestrial PGS, thereby assessing the probability that they will recolonize streams and riparian habitats locally extirpated by habitat alteration.

The Effects of Clearcut Logging

Amphibians are ectothermic animals with very thin, vascularized skin that serves as an ineffective barrier to water flow (Zug 1993). These physiological features make most amphibians intolerant of dramatic changes in moisture and temperature (Maiorana 1978, Jaeger 1980b, Welsh 1990). Low soil moisture, high ambient temperatures and exposure to dry air quickly lead to dehydration (Hutchinson 1961, Spotila 1972). Clearcutting dramatically alters the microclimatic conditions encountered at the forest floor. In comparison with interior forest habitat, clearcuts in Oregon and Washington have higher daily average air and soil temperatures, wind velocity and solar radiation, as well as lower average soil moisture and relative humidity (Chen *et al.* 1993, 1995, Brosofske *et al.* 1997). In coastal British Columbia, summer temperatures are slightly cooler and precipitation rates higher than those encountered in Oregon and Washington. The effects of clearcutting on microclimate may therefore be less severe in B.C. than further south, although comparable studies on microclimate have not yet been conducted. Temperature or moisture conditions found in clearcut habitat may fall outside the tolerance limits of some terrestrial amphibian species, leading directly to death. Even if the environmental conditions in clearcuts are not lethal to the species, increased risk of dehydration during periods of surface activity in clearcuts may force the salamanders to modify behaviours and spend extended periods of time in moist refuges to rehydrate. Clearcut environments could thereby limit individual fitness and population growth by restricting food intake and reproductive activity (Spotila 1972, Feder 1983).

The salamander genus *Dicamptodon* is considered part of an ancestral herpetofauna identified as the Old Northern Element (Savage 1960). These species are evolutionarily conservative and because of their long-term association with cool, moist Tertiary forests, are believed to be dependent upon the environmental conditions found only within these forests (Welsh 1990). *Dicamptodon* species such as the Pacific Giant

Salamander may, therefore, be particularly sensitive to habitat alterations. PGS found in Canada may also be particularly susceptible to perturbations because they are living at the northern extreme of their range (Johnson 1992).

Based on our limited knowledge about the natural history of terrestrial PGS and the microclimatic conditions found in clearcut habitat, I made several predictions about the effects of clearcutting on terrestrial PGS. First, I predicted that (1) terrestrial PGS population densities would be reduced in clearcuts relative to forested areas. I also predicted that (2) when terrestrial PGS were faced with a choice of habitat types, they would avoid clearcut habitat in favour of forested habitat, i.e., the forest/clearcut interface would act as a reflective barrier to terrestrial PGS movement. Finally, I predicted that (3) terrestrial PGS located in clearcut habitat would alter their behavior in a manner consistent with a mechanism that reduces their risk of desiccation. In comparison to salamanders located in forested habitat, I expected that animals found in clearcuts would reduce the amount of time they spent on the surface (i.e., increase refuge duration and decrease total area covered), remain closer to a source of water (stream) and restrict their movements to near-stream habitat, be more dependent on precipitation for their activity, be more nocturnal (i.e., restrict their movements to the night time), and alter their activity pattern seasonally (i.e., decrease their activity in summer and increase it in the fall).

The Efficacy of Riparian Buffer Strips

Riparian buffer strips are areas within a defined distance from a stream in which logging activities are restricted for stream protection purposes (Bren 1995). They effectively reduce the impacts of logging on stream systems by maintaining water quality, stream temperature, coarse woody debris, and invertebrate community composition, and by reducing sedimentation (Brown and Krygier 1970, Newbold *et al.* 1980, Beschta *et al.* 1987, Budd *et al.* 1987, Davies and Nelson 1994). These mitigative measures have proven effective in maintaining some fish populations at levels similar to those observed prior to forest harvesting (Murphy *et al.* 1986, Hartman *et al.* 1987, Davies and Nelson 1994). Buffered streams, therefore, likely provide an environment suitable for the development of aquatic PGS larvae and eggs. From a terrestrial point of view, the trees retained to form riparian buffer strips represent a source of leaf litter and new coarse woody debris, as well as providing shade, thereby maintaining soil moisture, relative humidity, air and soil temperatures (Brown and Krygier 1970, Bisson *et al.* 1987, O'Laughlin and Belt 1994, Brosofske *et al.* 1997). Riparian buffer strips have been effective in maintaining populations of some terrestrial mammal (e.g. Cross 1985) and bird species (e.g. Triquet *et al.* 1990), and likely provide habitat suitable for terrestrial amphibians such as PGS. The few studies that have investigated the efficacy of riparian buffer strips for preserving amphibian species suggest that sites with riparian buffer strips maintain population densities higher than clearcut sites without streamside protection (Steventon *et al.* 1996, Vesely 1996, but see Kelsey 1995).

Several studies of amphibian habitat associations indicate that habitat structure is a good predictor of amphibian abundance and diversity (Welsh 1990, Aubry and Hall 1991, Bury *et al.* 1991, Morrison *et al.* 1995). While clearcut areas have a habitat structure dramatically different from forested areas, the vegetation structure of riparian buffer strips in the Pacific northwest very closely resembles that found in unmanaged riparian forests (Vesely 1996). If forest structure is the essential component for maintaining amphibian populations, riparian buffer strips should be effective in preserving terrestrial PGS. I predicted that (1) the population density of terrestrial PGS at sites containing riparian buffer strips would be maintained at a level comparable to the density of terrestrial PGS at forested sites. I also predicted that (2) the behaviour of terrestrial PGS tracked at sites containing riparian buffer strips would not be significantly different from the behaviour observed at forested sites.

Dispersal Capability of the Terrestrial Pacific Giant Salamander

Amphibians are generally considered to be poor dispersers because of their relatively low mobility, their site fidelity, and the physiological limitations associated with being ectotherms with highly permeable skin (Blaustein *et al.* 1994). Anecdotal evidence from the Chilliwack River valley suggests that this may be the case for Pacific Giant Salamanders. Intensive stream searches revealed that only 20% or 30% of seemingly suitable streams in this valley contain PGS larvae (Farr 1985, Richardson and Neill 1995). I predicted that terrestrial PGS would be poor dispersers, with a very low probability of travelling sufficiently far to reach a neighbouring stream (approximately 500 m in the Chilliwack Valley).

METHODS

Radio Telemetry

To determine the effects of clearcut logging and riparian buffer strips on the behaviour of terrestrial PGS, and to determine the dispersal capability of this animal, I radio-tracked salamanders in various habitat types. I used a total of seven study sites in four different habitat types. Two second growth sites located in the Chilliwack valley were used in 1996. In 1997, two old growth sites, one site clearcut to the stream margin (cut age approximately 10 years), and two buffered sites (clearcut with a forested riparian buffer strip averaging 20 m and 30 m on either side of the stream), all located in the Nooksack Valley, were used. Refer to Chapter II for more details concerning the study sites. I radio-tracked a total of 20 salamanders: five in old growth habitat, six in second growth habitat, seven in riparian buffers and two in clearcut habitat. In 1996, I released each animal at the exact location where it had been captured. In 1997, I released all radio-tagged salamanders as close to their capture sites as possible, but at a standardised distance from the stream (25 m). This standard distance was approximately the average distance from the stream to the forest/clearcut interface at the buffered sites. At the two buffer sites, the salamanders were released at the actual forest/clearcut interface. These release locations were selected to determine the salamanders' response to the forest/clearcut interface at the buffered sites, and to standardise release protocol across the remaining sites. I recorded the location of each radio-tagged individual every second day. For each location, I measured distance to the stream and distance to the forest edge (at the buffered sites). See Chapter II for details regarding capture and radio-tagging methods, and tracking procedure.

Data Analysis

I performed an initial exploratory analysis to determine if the probability of salamander movement was associated with the habitat type in which the salamanders were found. I used a logistic regression analysis with movement (yes or no) and a categorical habitat variable (four categories, one for each habitat type), followed by post hoc comparisons of the model coefficients for each habitat type. I then added a variable for salamander size (mass) to the model to address my concern that salamander size could potentially confound the results of inter-habitat comparisons.

The Effects of Clearcut Logging

I used catch per unit effort data to make a very crude estimate of relative abundance of terrestrial PGS in the various habitat types. Catch per unit effort was calculated as the total number of terrestrial giant salamanders found per 100 person-hours of searching (e.g., if a team of two people spent four hours searching one night, this represented a total of 4 person-hours of searching). To test the prediction that salamanders would avoid clearcut habitat in favour of forested habitat, I focused on data collected for animals at the buffered sites (N = 7). Initially, I released each of these animals at the clearcut-forest interface. I used the Rayleigh test (Batschelet 1991) to test the null hypothesis that released animals moved randomly in all directions (alternative hypothesis: that there was a directionality to the salamander movements). I used direction of movement from the release location to the first observed refuge greater than 5 m from the release site as the metric. Subsequently, each time a salamander was located within approximately one average movement length of the edge (10 m) and then traveled sufficiently far to enable crossing into the clearrcut, I used their movement direction to determine whether they avoided clearcut habitats. If they traveled into clearcuts (crossed the “boundary”) less than would be expectd at random, then avoidance of clearcut habitat was inferred. I calculated the expected crossing frequency separately for each occasion as the proportion of a circle's arc for which that direction of travel would result in the salamander crossing the "boundary" into the clearcut (given the distance traveled in each case).

To test the prediction that salamanders at the clearcut site altered their behavior in a manner that would reduce the risk of desiccation, I compared a number of different behavioral measures across habitat types (clearcut, forested and buffered). An analysis of covariance (ANCOVA), with habitat type as the main effect and salamander mass serving as a covariate, was used for all data sets. The dependent variables used in these analyses were total area covered, mean movement length, mean refuge duration, seasonal activity level, diel activity pattern, mean distance from stream, and proportional use of near-stream versus upslope habitat. Data were transformed using log, arcsine square root and reciprocal transformations to meet the assumptions of normality and homogeneity of variances. Because of the very small sample sizes used in the ANCOVAs, I performed a power analysis for each non-significant result. To test the prediction that terrestrial PGS found in clearcuts would be more dependent on precipitation for their activity, I used a logistic regression analysis. Movement (yes or no) was used as the dependent variable, and both precipitation and habitat type were entered as categorical covariates along with habitat-rain interactions. By examining the model's predicted probability of movement with and without rain in each of the habitat types, I calculated the relative dependence of salamanders in each habitat type upon rainfall for their activity.

The Efficacy of Riparian Buffer Strips

Once again, I used catch per unit effort data to make a crude comparison of the relative abundance of terrestrial PGS in riparian buffers and in sites with continuous forest. Using the data collected at old growth and second growth sites, I calculated the proportion of the salamanders' "normal" activities in forested habitat that fell within hypothetical riparian buffer zones 20 m and 40 m in width. I chose to investigate a 40 m buffer zone because a draft copy of the Pacific Giant Salamander species report from the *Managing for Identified Wildlife Guidebook* proposed maintaining wildlife habitat areas no less than 40 m wide along selected streams with known PGS populations. I also chose to look at a 20 m buffer zone because current regulations outlined in the *Riparian Management Area Guidebook* for the B.C. Forest Practices Code (B.C. Ministry of Environment and B.C. Ministry of Forests 1995) require a minimum management zone (albeit discretionary) of at least 20 m along fishless headwater streams (S5 and S6).

To test the prediction that terrestrial PGS inhabiting riparian buffer strips would not change their movement behaviour from that observed in forested sites, I used ANCOVAs with habitat type as the main effect and salamander mass serving as a covariate.

Dispersal Capability of the Terrestrial Pacific Giant Salamander

To investigate the dispersal potential of terrestrial PGS, I focused on the data collected during the first two months of tracking after each animal had been released. I did this in order to include all 20 animals in the analysis (because animals were followed for various lengths of time). To determine the dispersal potential of each animal, I calculated the cumulative distance travelled during the two month period. Because salamanders do not tend to move continually in one direction, I also calculated the actual straight line (displacement) distance between each animals' release site and its location after two months of tracking. This gave a more realistic estimate of dispersal probability. I used ANCOVAs, with habitat type as the main effect and salamander mass as the covariate, to assess the effect of habitat type on the dispersal potential (cumulative distance) and dispersal probability (displacement distance) of terrestrial PGS. I then subdivided the displacement distance into eight equally sized categories and fit a model to the frequency distribution of displacement distance after two months. I used this model to predict the probability of an animal dispersing various distances over a two-month period.

RESULTS

The initial exploratory logistic regression analysis indicated that salamander movement (moved versus did not move) was associated with a categorical habitat variable ($X^2 = 22.471$, df = 3, $P = 0.0001$). This suggests that the probability of movement was associated with the habitat type in which the salamander had been found. *Post hoc* comparisons of the model coefficients for each habitat type indicated that the difference in movement probability was only statistically significant when comparing the second growth habitat type with each of the other three habitat types (old growth, buffered and clearcut) (t-tests, $P < 0.02$). That is, animals found in second growth habitat (observed in cool, wet 1996) had a higher probability of moving than animals found in the other habitat types (all observed in warmer, dryer 1997). Adding a salamander mass variable to the logistic model did not result in a significant model improvement ($X^2 = 0.003$, $P = 0.95$). Therefore, the probability of movement was not associated with salamander size. This result allayed my concern that the distribution of animals of different sizes within the habitat types would influence the results of inter-habitat comparisons.

The Effects of Clearcut Logging

Catch per unit effort data suggested that terrestrial PGS may be less abundant in clearcuts than in old growth habitat (7.4 versus 13 salamanders caught per 100 person-hours of searching). As with all catch per unit effort data, it is difficult to rule out the possible effects of varying "search efficiency" in different habitat types.

The Rayleigh test conducted on the initial movement of each animal released at the clearcut-forest interface ($N = 7$) revealed that the salamanders did not move in a random direction ($z = 3.35$, $P < 0.05$). On average, they moved directly away from the clearcut and into the forest, as indicated by the mean movement angle in Figure 3.1. The interface between forested habitat and clearcut did not act as a complete barrier to terrestrial PGS movement, however. Three of the seven (43%) animals tracked at buffered sites crossed this "boundary" at some point during the study period. Excursions into clearcut areas were fairly brief (maximum of eight days). Not including release sites, salamanders came within 10 m of the clearcut boundary (and subsequently travelled sufficiently far to enable crossing into the clearcut) on only five occasions (three individuals) over the course of the study period. Under these conditions, only on one occasion (20%) did the salamander actually leave the forest and travel into the clearcut.

Totalled over the five occasions, the expected frequency of boundary crossing assuming travel in a random direction was 1.89 times. This is nearly twice the frequency actually observed, suggesting that (based on a *very* small sample size) the salamanders were avoiding the clearcut when travelling near the forest edge.

To compare the behaviour of terrestrial PGS in clearcuts to that of animals at forested sites, I conducted a series of ANCOVAs with habitat type as the main effect and salamander mass serving as a covariate. There was no significant difference between habitat types in the total area covered during the tracking period (95% adaptive kernel estimate) ($F_{3,12} = 0.47$, $P = 0.71$, $N = 20$, power = 0.1). Figure 3.2 indicates that there was huge variation in the area covered by individuals in old growth habitat (ranging from 403 m^2 – 35,321 m^2), and that animals in clearcut habitat tended to cover a smaller area. There was no significant difference between the habitat types in the average length of movement (once initiated) ($F_{3,12} = 1.37$, $P = 0.30$, $N = 20$, power = 0.3) (Figure 3.3). An analysis comparing the average refuge duration also indicated that there was no significant difference between habitat types ($F_{3,12} = 0.26$, $P = 0.86$, $N = 20$, power = 0.1). Figure 3.4 suggests that the animals in both second growth and buffered sites tended to move more frequently than the animals in either old growth or clearcut sites. The relatively long average refuge duration depicted for old growth sites was largely influenced by one animal (#21 at the Glacier site) that remained stationary for nearly a month at the beginning of the study period. With the exception of this individual, animals in the clearcut habitat appeared to have a longer refuge duration than the animals in the forested habitat.

To investigate the effects of seasonality, I compared differences in mean movement length during the summer and fall. I found no significant difference between habitat types ($F_{3,12} = 1.62$, $P = 0.24$, $N = 20$, power = 0.3). The smallest difference between summer and fall movement lengths occurred at the second growth sites, but there was no difference between any of the other habitat types (Figure 3.5). I also found no significant difference between habitat types when comparing the difference in refuge duration between the summer and fall ($F_{3,12} = 0.08$, $P = 0.97$, $N = 20$, power = 0.1). Here, the trend was for the smallest seasonal effect occurring at the second growth sites and the greatest seasonal effect occurring at the clearcut (Figure 3.6). As noted earlier, the relatively large average seasonal difference evident in the figure for old growth sites was largely influenced by one animal (#21 at the Glacier site) that remained stationary for nearly a month during the summer of 1997.

Examination of the diel activity pattern of the salamanders indicated no significant difference between the proportion of nocturnal movements made by salamanders tracked in different habitat types ($F_{3,9} = 0.69$, $P = 0.58$, $N = 17$, power = 0.1). Figure 3.7 suggests that animals found at the second growth sites tended to be the least nocturnal of all the habitat types. I found no significant difference between the animals at different habitat types in average movement length made at night versus during the day ($F_{3,9} = 0.52$, $P = 0.98$, $N = 17$, power = 0.1). Figure 3.8 suggests that animals found at the clearcut site had the smallest difference in movement length during the daytime and at night. This trend was based on a total of four movements (three made by one animal and one by another), making it difficult to determine whether this was a reliable trend or simply a product of small sample size.

I found no significant difference between habitat types in the average distance salamanders were found from the stream ($F_{3,12} = 0.81$, $P = 0.52$, $N = 20$, power = 0.2). Comparing the habitat types graphically, however, revealed a trend towards shorter distances from the stream at the clearcut site than at forested sites (Figure 3.9). Statistical analyses also indicated that there was no significant difference between habitat types in the proportion of observations made in near-stream habitat (versus in upslope habitat) ($F_{3,12} = 0.70$, $P = 0.58$, $N = 20$, power = 0.1). Graphical comparison of the habitat types revealed that 100% of observations in the clearcut were made in near-stream habitat, while in the other three habitat types on average 25% to 45% of the observations were made in upslope areas (Figure 3.10).

To assess the relative influence of precipitation on salamanders in different habitat types, I performed a logistic regression analysis. Adding a categorical habitat variable along with habitat-rain interactions to the model indicated that salamander movement was associated with rainfall ($X^2 = 28.61$, df = 6, $P < 0.001$). Looking at the model's predicted probability of movement with and without rain in each of the habitat types, I found that salamanders in second growth habitats were 1.16 times more likely to move after rainfall than when no rain had been recorded in the preceding 48 hours. In buffered habitats, the increase in movement probability with rain was 1.48 times. In old growth habitats it was 1.76 times, and in clearcuts the increase was 2.79 times. These results suggest that the movement of salamanders was much more dependent upon rainfall in clearcuts than in the other three habitat types (nearly two fold) (Figure 3.11).

The Efficacy of Riparian Buffer Strips

Catch per unit effort data suggested that riparian buffers maintained terrestrial PGS at similar levels to those found in old growth areas (12 and 13 salamanders caught per 100 person-hours of searching in the two habitat types respectively). Averaged across all animals radio-tracked in forested areas (old growth and second growth, N=10), 87.6 ± 6.1% (mean ± SE) of salamander observations were recorded within a hypothetical 40 m buffer, and 79.4 ± 7.8% within a 20 m buffer.

Results from the ANCOVAs indicated that salamanders tracked at riparian buffer strips did not behave significantly differently from animals in forested sites (old growth or second growth) with respect to total area covered ($F_{3,12} = 0.47$, $P = 0.71$, $N = 20$, power = 0.1), movement length ($F_{3,12} = 1.37$, $P = 0.30$, $N = 20$, power = 0.3), refuge duration ($F_{3,12} = 0.26$, $P = 0.86$, $N = 20$, power = 0.1), seasonal activity level ($F_{3,12} = 0.08$, $P = 0.97$, $N = 20$, power = 0.1), diel activity pattern ($F_{3,9} = 0.69$, $P = 0.58$, $N = 17$, power = 0.1), distance from stream ($F_{3,12} = 0.81$, $P = 0.52$, $N = 20$, power = 0.2), and proportional use of near-stream versus upslope habitat ($F_{3,12} = 0.70$, $P = 0.58$, $N = 20$, power = 0.1) (Figures 3. 2 to 3.10).

Dispersal Capability of the Terrestrial Pacific Giant Salamander

Despite the apparently sedentary nature of terrestrial PGS, they were capable of moving reasonably large distances in a short period of time. The maximum recorded distance travelled between checks (48 h) was 67 m. When I focussed on the first two months of tracking each animal, the maximum cumulative distance travelled was 310 m (ranging from 44 m – 310 m). Out of the 20 radio-tagged animals, four (20%) had a cumulative distance travelled greater than 200 m, and 11 (55%) greater than 100 m. When I calculated the actual straight-line displacement distance between each salamander's release site and its locations after two months, only one of the 20 radio-tagged animals (5%) had a displacement distance greater than 200 m. An ANCOVA indicated that there was no significant difference in the straight-line displacement distance between habitat types ($F_{3,12} = 1.84$, $P = 0.19$, $N = 20$). The frequency distribution of the straight line displacement distance after two months (Figure 3.12) fit the negative exponential model $y = a \times [e^{b(x)}]$, where $a = 12.26$ and $b = -1.26 \times 10^{-2}$ ($R^2 = 0.94$, $F = 59.64$, $P = 0.002$). I used this model to estimate the predicted probability of an animal dispersing various distances over a two-month period (Table 3.1). The predictions from this model suggested that an animal had about a probability of one in 100 of dispersing 300 m in a two-month period, about a one in 1,000 likelihood of dispersing 500 m, and a probability of only about two in a million of dispersing a kilometre.

DISCUSSION

The Effects of Clearcut Logging

Results of this study were ambiguous. Some measures indicated that the behaviour of terrestrial PGS remained unaltered in clearcut habitat (e.g., average movement length, proportion of nocturnal movements, seasonal variation in movement length). However, many other subtle, yet potentially important, differences were found between clearcut and forested habitats. These minor differences suggested that clearcut logging may adversely affect terrestrial PGS. Small sample sizes and high within-site variability made it difficult to determine whether statistically non-significant results were due to a lack of behavioural differences between salamanders in different habitat types or simply to low statistical power. As a result, most effects were detected by observing trends in the data.

Catch per unit effort data were consistent with my prediction that terrestrial PGS population densities would be reduced in clearcuts relative to forested areas. Several earlier studies comparing amphibian relative abundance, density, or species richness between harvested and mature or old-growth stands have also found depauperate assemblages of terrestrial amphibians in disturbed areas (Bury 1983, Pough *et al.* 1987, Petranka *et al.* 1993, Dupuis *et al.* 1995, Vesely 1996). Possible mechanisms behind the declines following logging include direct mortality during logging operations, increased physiological stress caused by the removal of shading, reduction in cover objects such as leaf litter and woody debris, increased stream sedimentation destroying nesting sites and aquatic larval habitat, and egg mortality caused by increased water temperatures (Pough *et al.* 1987, Corn and Bury 1989, Welsh 1990, Petranka *et al.* 1993, Dupuis *et al.* 1995). An alternative explanation is that amphibians do not actually decline following clearcutting, but are simply less active (i.e. Figure 3.4) and therefore are captured less frequently. My results based on catch per unit effort data do not necessarily indicate that salamander density was actually lower in clearcut habitat relative to forested areas. In the late spring and early summer in clearcut habitat, understorey vegetation, particularly fire weed (*Epilobium angustifolium*), grew up making it much more difficult to see the ground when searching for salamanders. It is possible that this difference in "search efficiency" at clearcut and forested sites accounted, at least in part, for the difference in catch per unit effort recorded at these habitat types. Also, because using catch per unit effort data was not an original goal of the project, I made no deliberate attempt to standardise search method across sites. While about 10 m of forest floor was searched on each side of the stream at forested sites, at clearcut sites the search was confined within the stream itself and right along its margin. Since terrestrial PGS appear to be highly concentrated in near-stream habitat in clearcuts, this inconsistency in search method could result in an overestimation of the abundance of salamanders in clearcut habitat relative to forested habitat. Bias was also likely a problem in previous studies comparing salamander relative abundance, density, or species richness because the capture techniques employed (pitfall trapping and area constrained searches) would also have been heavily influenced by habitat type.

Although I observed terrestrial PGS "crossing" from forested habitat to clearcut habitat, this occurred infrequently (a total of three times), and on every occasion the salamander returned to forested habitat within a maximum of eight days. In addition, one of the animals captured at the clearcut site travelled across the clearcut (102 m) and entered forested habitat. As I had predicted, when salamanders were faced with a choice between forested and clearcut habitats, they tended to avoid clearcuts in favour of the forest. The forest edge, therefore, appeared to act somewhat as a reflective barrier to the movement of terrestrial PGS. This finding was especially important in that these animals did not inhabit a confined home range, but rather wandered throughout their surroundings restricted solely by the area of suitable habitat (see Chapter II). Since clearcuts appear to represent a boundary of suitable habitat to wandering PGS, clearcutting potentially reduces the inhabitable area of all the terrestrial PGS found in the region.

I predicted that terrestrial PGS located in clearcut habitat would change their behaviour in a manner consistent with reducing their risk of desiccation. To address this question, I compared several behavioural measures between animals tracked in clearcut habitat and those tracked in forested areas. One problem with this analysis was the confounding effect of year and second growth habitat type. The spring and summer seasons in 1996 were much cooler and wetter than those of 1997. Because all data for second growth habitat were collected in 1996, while the rest of the data was collected in 1997, I was unable to determine whether differences in the behaviour of animals tracked in 1996 and in 1997 were due to differences in habitat type or to differences in weather. In order to resolve this problem, I should have collected all data to be used in habitat comparisons concurrently. In addition, I was only able to capture two animals sufficiently large to implant a transmitter at one clearcut site during this study. This severely limited my ability to draw conclusions about the effects of clearcutting on the behaviour of terrestrial PGS found in this habitat type.

As I had predicted, salamanders found in clearcut habitat appeared to alter their behaviour in ways that would reduce their risk of desiccation. Animals tracked at the clearcut site tended to remain in their refugia for longer periods of time, and covered smaller areas than did animals in forested areas. Clearcut animals also remained closer to the stream, with no recorded refuge locations greater than 5 m from the water's edge. The activity of animals found in the clearcut were more dependent on precipitation and on season than the activity of animals found in the forest. These changes in behaviour, particularly the reduction in time spent at the surface, could impact the ability of animals inhabiting clearcut habitat to find food and/or mates. For example, Fraser (1976) showed that plethodontid salamanders living underground were at an energetic disadvantage compared to those on the surface because consumption of prey was limited underground. Similarly, Jaeger (1980b) showed that ambient moisture regulated food availability of plethodontid salamanders in the eastern U.S., and ambient temperature set the metabolic requirements of the salamanders. Food was more limiting in dry than in wet conditions, and metabolic needs were higher in warm than in cool conditions. To assess the impacts of behavioural modifications exhibited by terrestrial PGS found in clearcut habitat, the relative availability of such factors as food, moisture and mates must be determined in forested and clearcut areas.

The Efficacy of Riparian Buffer Strips

My results indicated that riparian buffer strips may serve as an effective management strategy for the conservation of terrestrial PGS. Most (88%) of the terrestrial PGS telemetry locations recorded in forested habitat fell within a hypothetical 40 m wide riparian buffer strip. Decreasing the width of the buffer strip to 20 m on either side of the stream still maintained 79% of the telemetry locations within the buffer strip. From my analyses I was not able to determine the influence of buffer width on salamander abundance. Future studies should address this issue before narrow buffer widths are recommended for the conservation of terrestrial PGS.

The preceding arguments were based upon data collected in continuous forest. In drawing these conclusions, therefore, I assumed that a riparian buffer strip provided habitat comparable to that found in the interior of a forest stand. Previous work has shown, however, that microclimatic conditions are actually quite different near a forest edge than in the forest interior because of changes in solar radiation, wind velocity, relative humidity, and soil moisture (Chen *et al.* 1993, 1995, Brosofske *et al.* 1997). These edge effects negatively impact many species that require protected forest conditions (Lovejoy *et al.* 1986, Rosenberg and Raphael 1986, Yahner 1988). Although studies conducted to date have focused on avian and mammalian species, edge effects likely influence some amphibian species, particularly given their susceptibility to desiccation. One study investigating the effects of forest edge on habitat use by Amazonian frogs, however, showed that despite an increase in temperature and a decrease in humidity at the forest edge, patterns of habitat use were independent of proximity to forest edge (Gascon 1993). The microclimatic changes associated with forest edges, therefore, may not be sufficient to alter habitat use in some amphibian species.

I predicted that the population density of terrestrial PGS in riparian buffer strips would be maintained at a level comparable to that found in forested sites. Catch per unit effort data were consistent with this prediction. I also predicted that terrestrial PGS located at sites containing riparian buffer strips would not change their behaviour from that observed at forested sites. Results from the inter-habitat comparisons corroborate this prediction. Although the power of the inter-habitat analyses to detect a difference between buffered and forested sites was very low, careful examination of the data revealed no trends that suggest that terrestrial PGS in riparian buffer strips behaved differently from animals in forested habitat (Figures 3.2 to 3.10). This may be surprising in light of evidence from southern Oregon that microclimatic edge effects (changes in air temperature, relative humidity, solar radiation and wind speed) likely extend well into or throughout riparian buffer strips of widths used in my study (Chen *et al.* 1993, 1995). The milder, wetter climate of coastal British Columbia and northern Washington may reduce the severity of these edge effects, or decrease the distance the effects reach into the forest. My results suggest that in this study area, edge effects encountered in 20 m and 30 m buffer strips did not lead to microclimatic conditions outside the range of tolerance of terrestrial PGS. Therefore, if clearcut habitat does pose a threat to terrestrial PGS populations, maintaining forest structure along the stream channel may be sufficient for the preservation of these animals.

Studies examining the effects of riparian buffer strips on amphibian populations have been undertaken only in the last few years. One study found that even with the retention of buffer strips, *Ascaphus truei* tadpole density was negatively affected by timber harvest (Kelsey 1995). The remaining studies concluded that forested buffer strips maintained both terrestrial (Vesely 1996) and aquatic (Steventon *et al.* 1996) amphibian population densities higher than those found at sites clearcut to the stream margin. One study found amphibian densities to be even higher at buffered sites than at sites with continuous forest (Wahbe 1996). This is consistent with my findings that indicated a slight trend for terrestrial PGS in riparian buffer strips to be more active (with shorter average refuge duration and longer movement lengths) than animals found in old growth habitat (Figures 3.3 and 3.4). These results may be explained by the increased shading in riparian buffer strips caused by a slight increase in low shrub cover at this habitat type over areas of continuous forest (Kinley and Newhouse 1995, Vesely 1996).

Dispersal Capability of the Terrestrial Pacific Giant Salamander

My results indicated that while terrestrial PGS are capable of travelling long distances, the probability of dispersal to a new stream was quite low. In the Chilliwack River valley the distance between neighbouring streams is extremely variable, but on average it is approximately 0.5 km (pers. obs.). Results of the dispersal probability model suggested that the probability of any given salamander travelling this distance in a two-month period was about one in a thousand. While this estimate appears relatively high, it is undoubtedly a great overestimation. First, this model assumed that mortality risk (e.g., predation) of salamanders did not increase during dispersal. In addition, the dispersal probabilities were based upon movements made in all directions (not simply those perpendicular to the stream of origin). If movement distances were weighted by the angle to a neighbouring stream, the probability of an animal dispersing to an adjacent stream 0.5 km away would be significantly less than one in a thousand. Finally, successful dispersal requires that the neighbouring stream provide suitable Giant Salamander habitat (e.g., a permanent stream that is able to support larval PGS). Even if the terrestrial PGS population density in an area is relatively high, these numbers suggest that over the short term, little long-range dispersal will occur. These findings are supported by evidence from intensive stream searches in the Chilliwack Valley that indicated only 20% or 30% of seemingly suitable streams contained PGS larvae (Farr 1985, Richardson and Neill 1995). The findings are also consistent with the generally held belief that amphibians are poor dispersers and may take several decades to recolonise areas that have been locally extirpated (Corn and Bury 1989, Sjogren 1991, Petranka *et al.* 1993, Blaustein *et al.* 1994).

The conclusions I have drawn above may be slightly pessimistic for two reasons. First, all salamander movement data used in developing the dispersal model were collected during the summer and fall. Nothing is known about the activity of terrestrial PGS in the spring. It is possible that spring is the time when salamanders disperse, in which case including data collected during the spring in my analyses would have resulted in higher dispersal probabilities. Secondly, because I was implanting radio transmitters intraperitoneally, I was only able to study animals with a mass of 25 g or greater. Terrestrial *Dicamptodon* salamanders as small as 10 g have been found (pers. obs.). In many species, including some amphibians, it is the juvenile animals that are responsible for the majority of the dispersal (Horn 1983, Duellman and Trueb 1986). If this were the case for Pacific Giant Salamanders, including smaller animals in my analyses would also have increased the estimated dispersal probabilities.

Table 3.1. The probability of any given terrestrial Pacific Giant Salamander dispersing various distances over a two-month period based on the negative exponential model $y = a \times [e^{b(x)}]$, where $a = 12.26$ and $b = -1.26 \times 10^{-2}$.

distance (m)	probability of moving this distance in two months	
0	0.61	
100	0.27	
200	0.05	
300	0.01	(one in a hundred)
400	3.9×10^{-3}	
500	1.1×10^{-3}	(one in a thousand)
1000	2.1×10^{-6}	(two in a million)

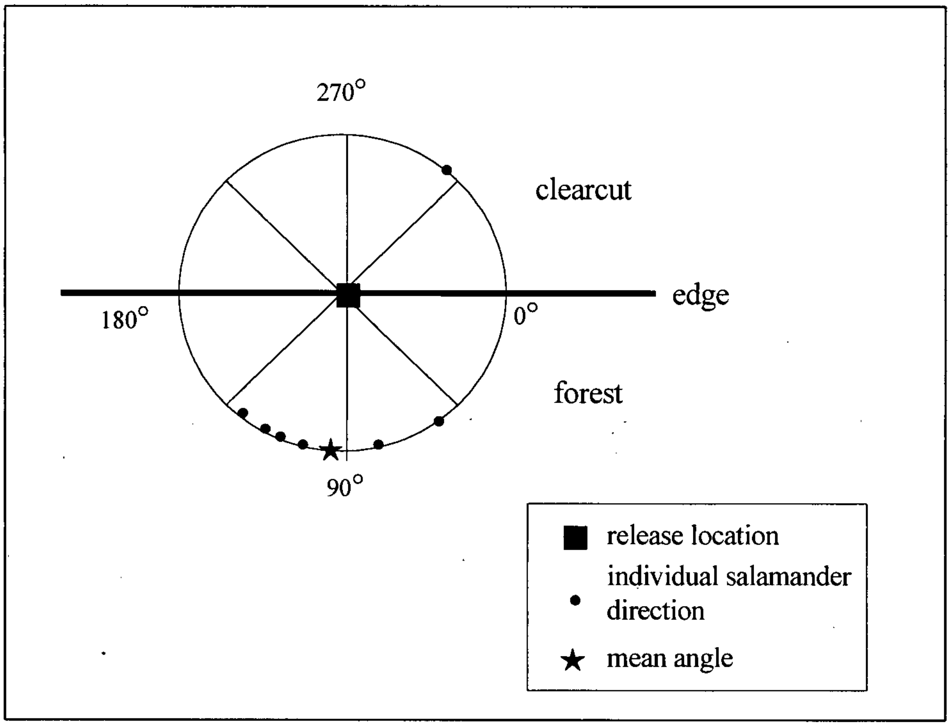

Figure 3.1. Circular scatter plot showing the initial post-release movement direction of each salamander at the buffered sites (N = 7) and the mean angle of movement (all animals together).

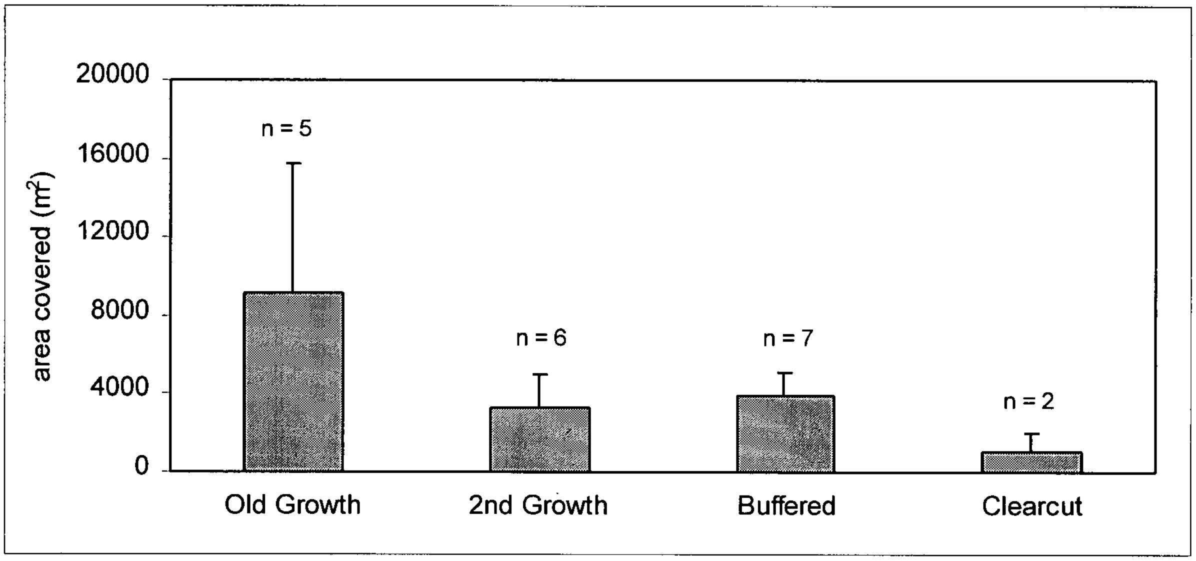

Figure 3.2. Mean area covered (calculated using a 95% adaptive kernel estimate) by salamanders in each habitat type. Error bars are one standard error of the mean.

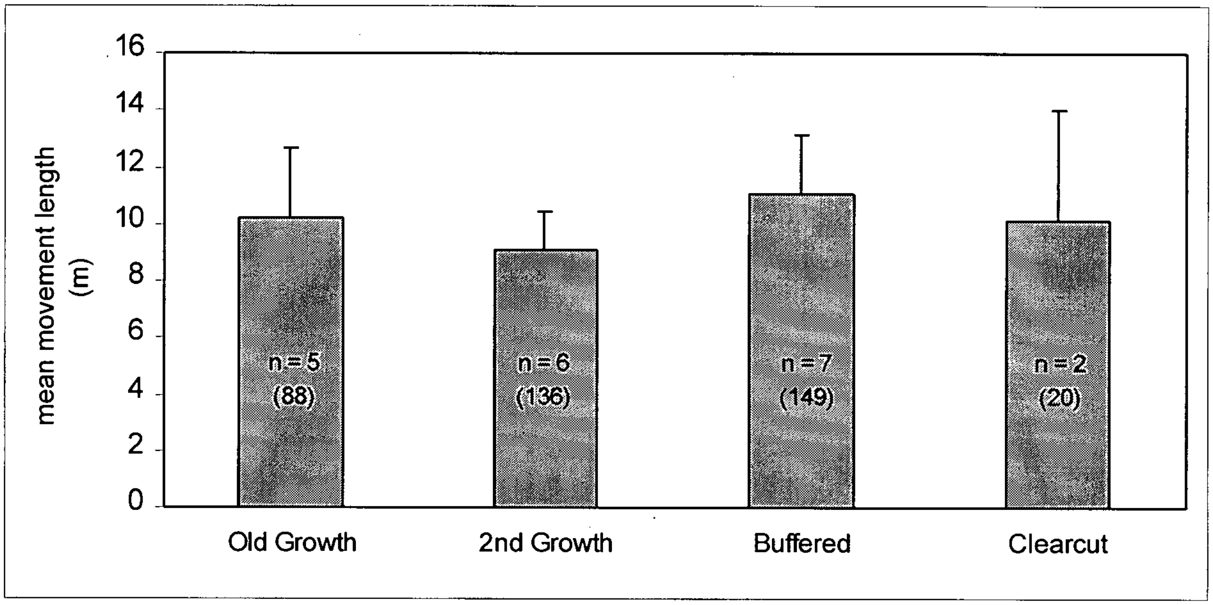

Figure 3.3. The mean movement length (once initiated) made by terrestrial Pacific Giant Salamanders in each habitat type. Error bars are one standard error of the mean. Numbers in brackets indicate the total number of movements from which the means were calculated.

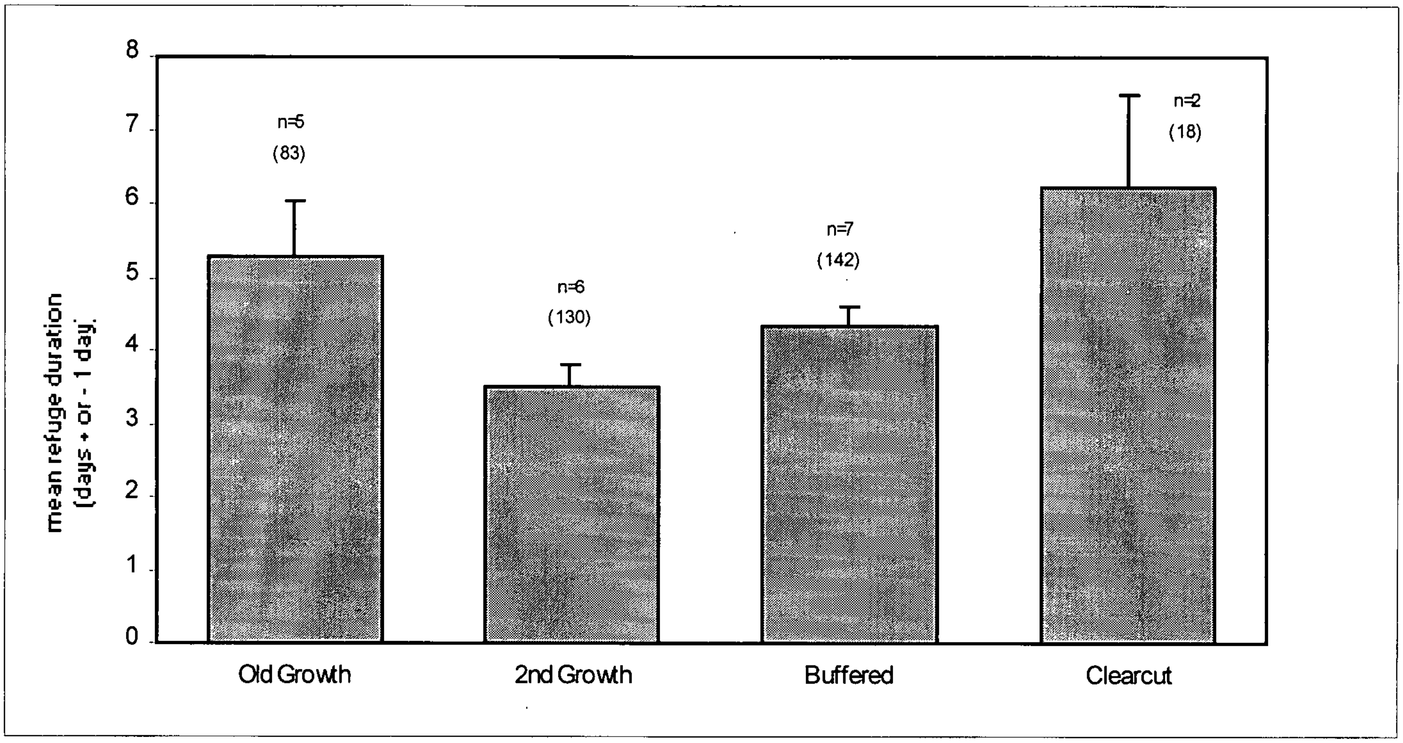

Figure 3.4. The mean refuge duration (number of days between movements) of terrestrial Pacific Giant Salamanders in each habitat type. Error bars are one standard error of the mean. Numbers in brackets indicate the total number of refuge periods from which the means were calculated.

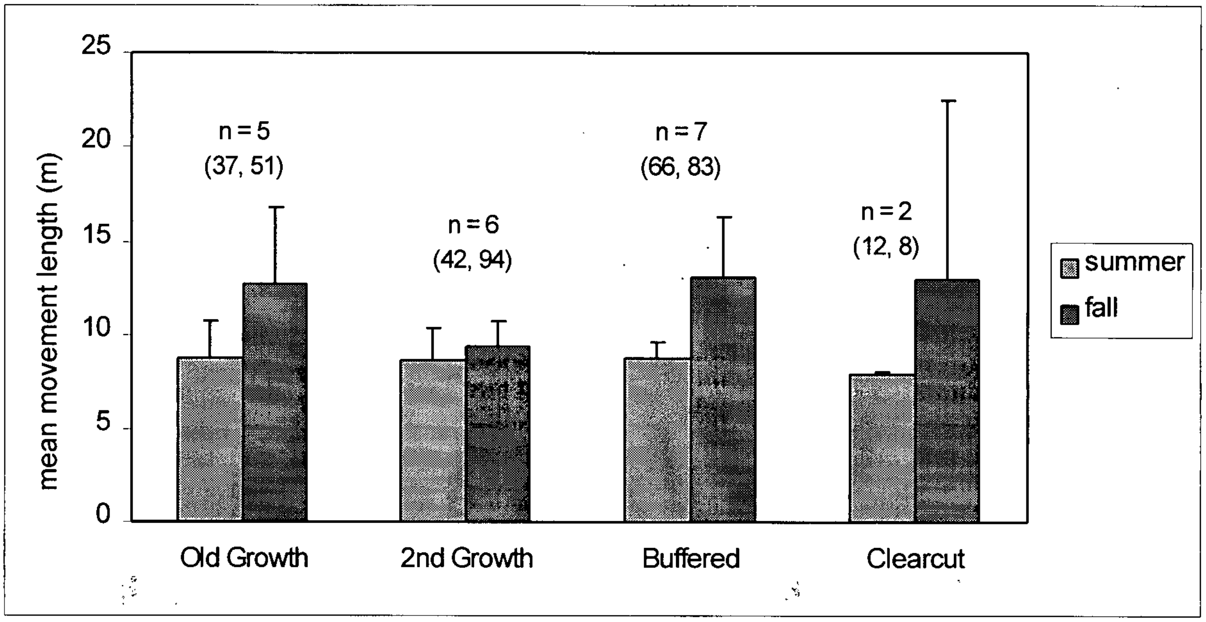

Figure 3.5. Mean length of movements (once initiated) made during the summer and fall by terrestrial Pacific Giant Salamanders at each habitat type. Error bars are one standard error of the mean. Numbers in brackets indicate the total number of movements from which the means were calculated (summer, fall).

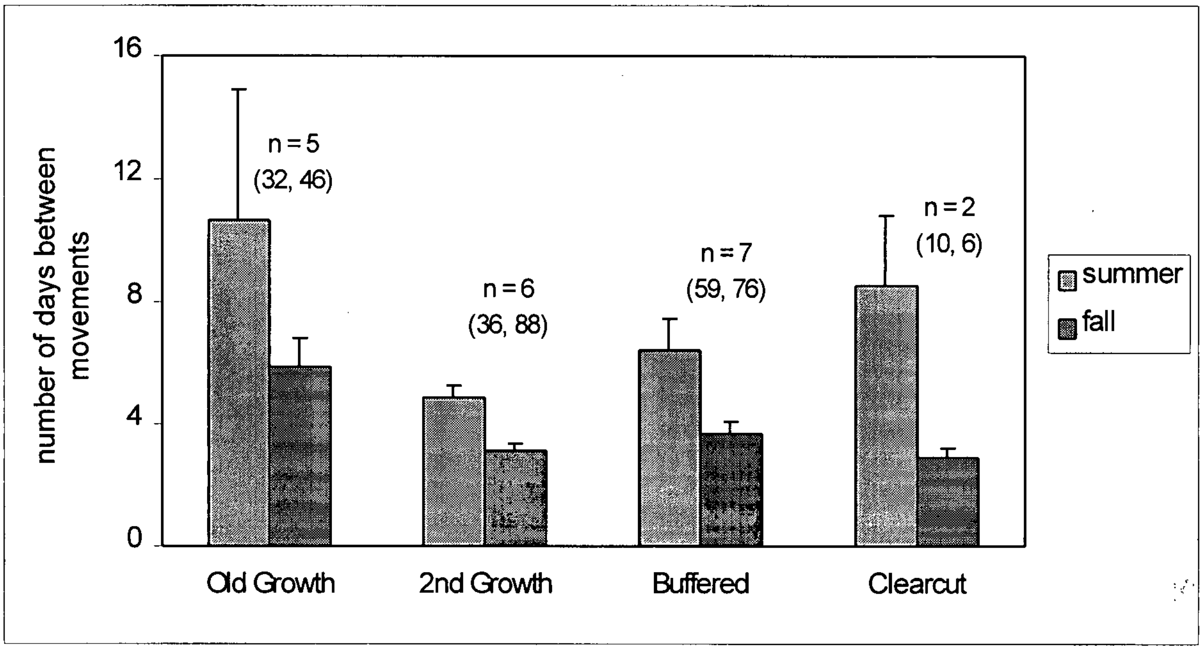

Figure 3.6. Mean refuge duration during the summer and fall for terrestrial Pacific Giant Salamanders at each habitat type. Error bars are one standard error of the mean. Numbers in brackets indicate the total number of refuge periods from which the means were calculated (summer, fall).

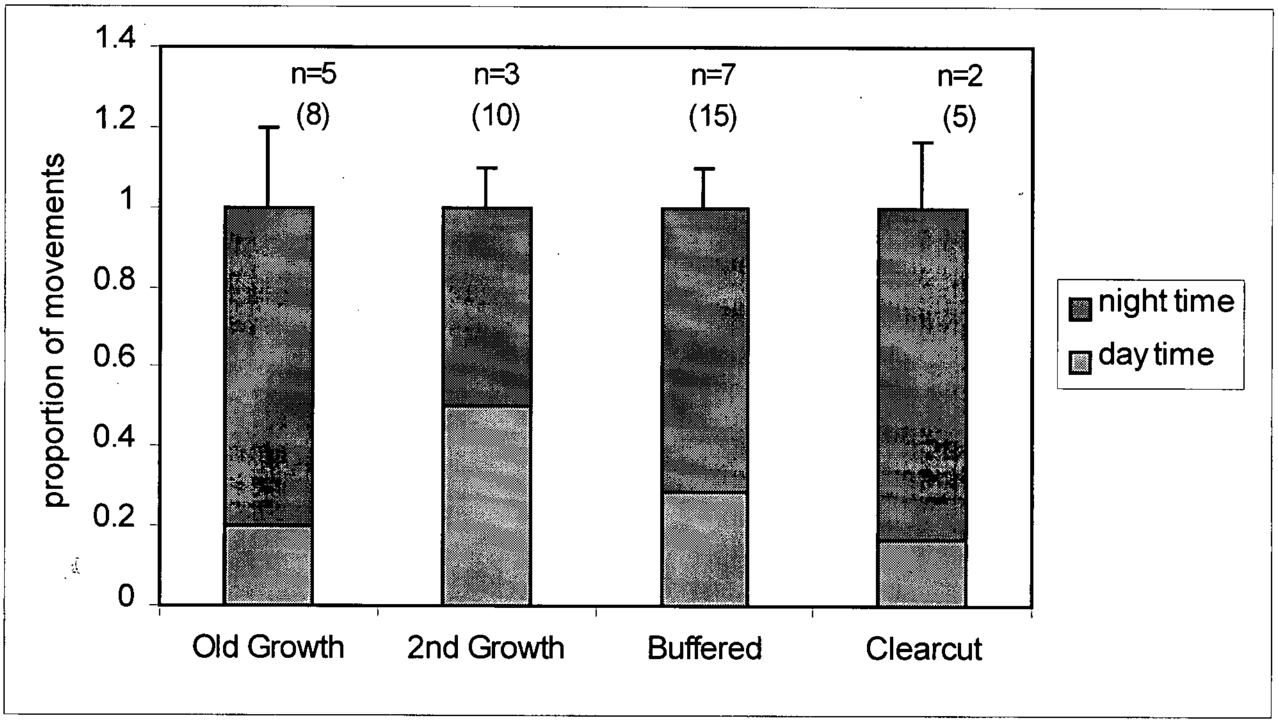

Figure 3.7. Proportion of movements made during the day and night by terrestrial Pacific Giant Salamanders at each habitat type. Error bars are one standard error of the mean. Numbers in brackets indicate the total number of movements from which the proportions were calculated.

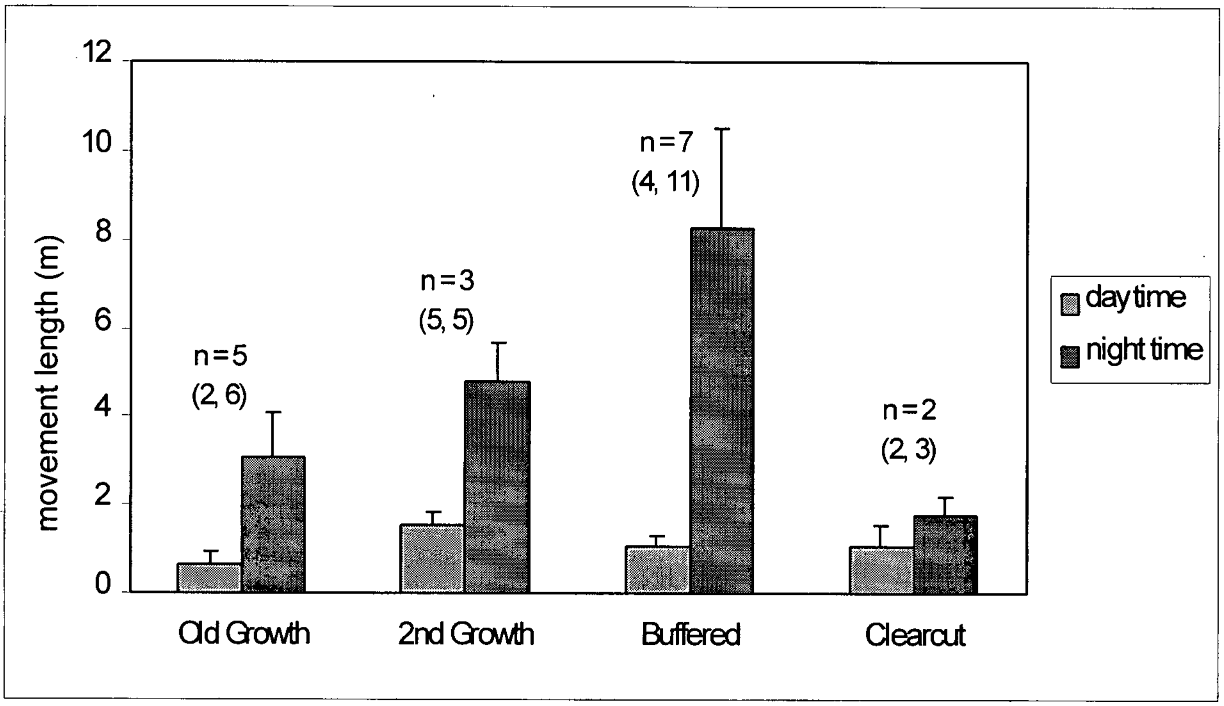

Figure 3.8. Mean daytime and nighttime movement lengths (once initiated) for terrestrial Pacific Giant Salamanders at each habitat type. Error bars are one standard error of the mean. Numbers in brackets indicate the total number of movements from which the means were calculated (day, night).

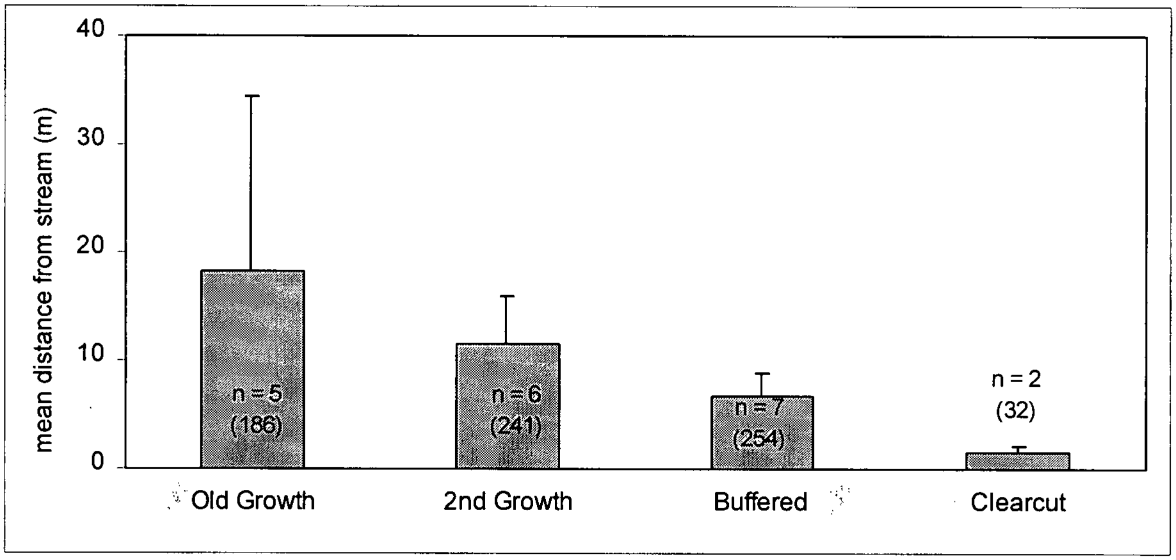

Figure 3.9. Mean distance from the stream that terrestrial Pacific Giant Salamanders were located in each habitat type. Error bars are one standard error of the mean. Numbers in brackets indicate the total number of telemetry locations from which the mean distances were calculated.

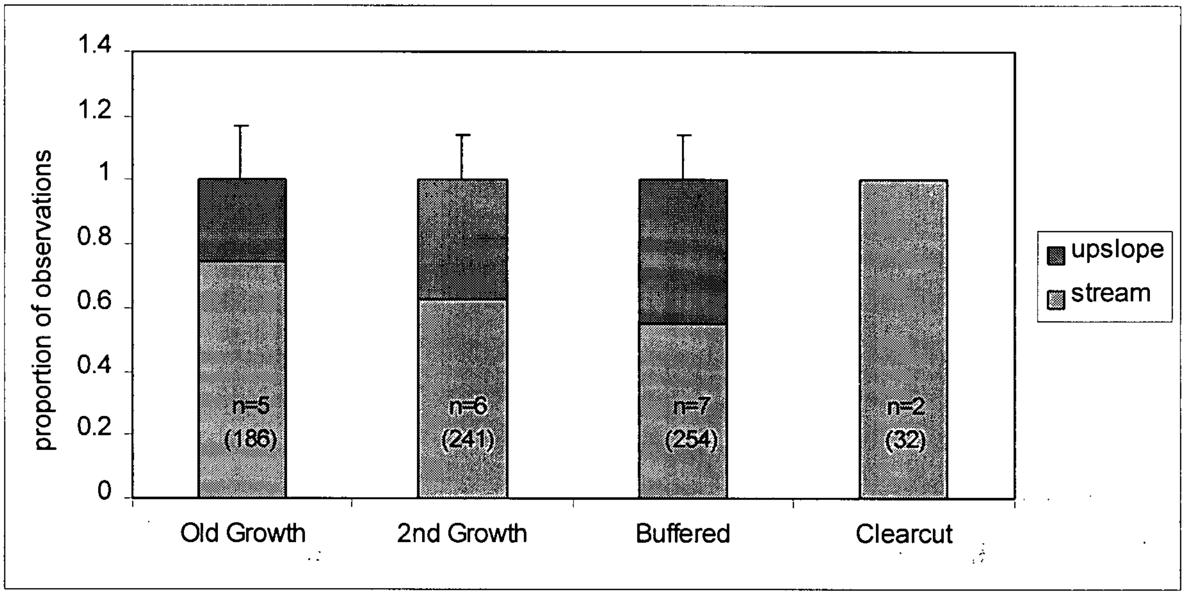

Figure 3.10. Proportion of salamander locations recorded in near-stream (< 5 m from the water's edge) and upslope (> 5 m from the water's edge) areas at each habitat type. Error bars are one standard error of the mean. Numbers in brackets indicate the total number of telemetry locations from which the proportions were calculated.

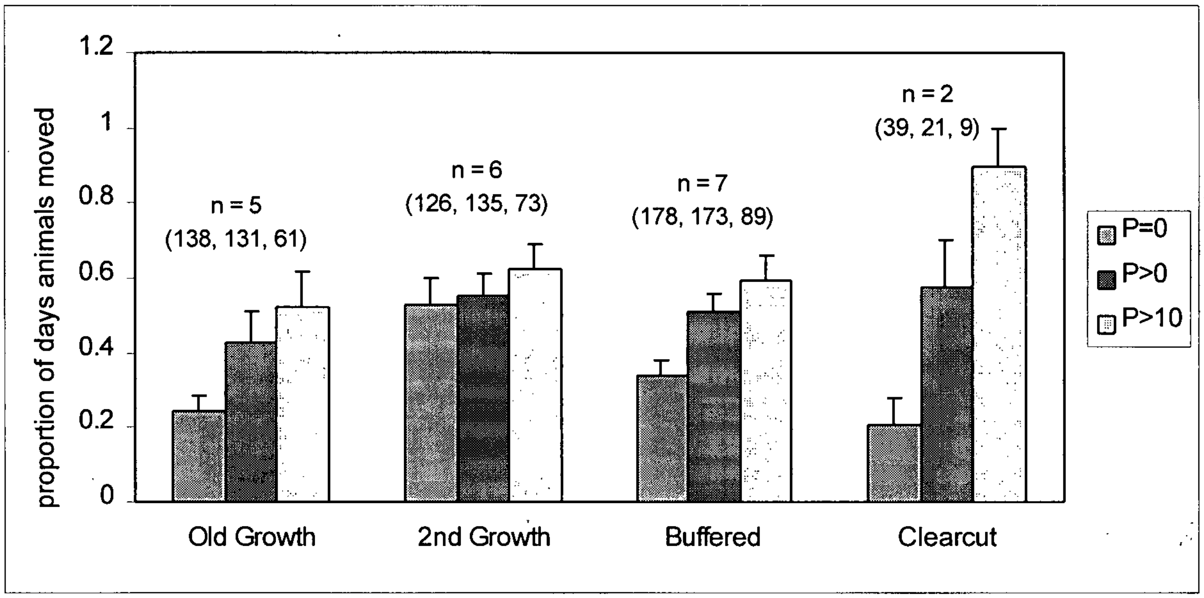

Figure 3.11. The proportion of days when there was no precipitation (P = 0), some precipitation (P > 0), and heavy precipitation (P >10 mm) on which terrestrial Pacific Giant Salamanders moved at each habitat type. Error bars are one standard error of the mean. Numbers in brackets indicate the total number of days from which the proportions were calculated (P = 0, P > 0, P > 10 mm).

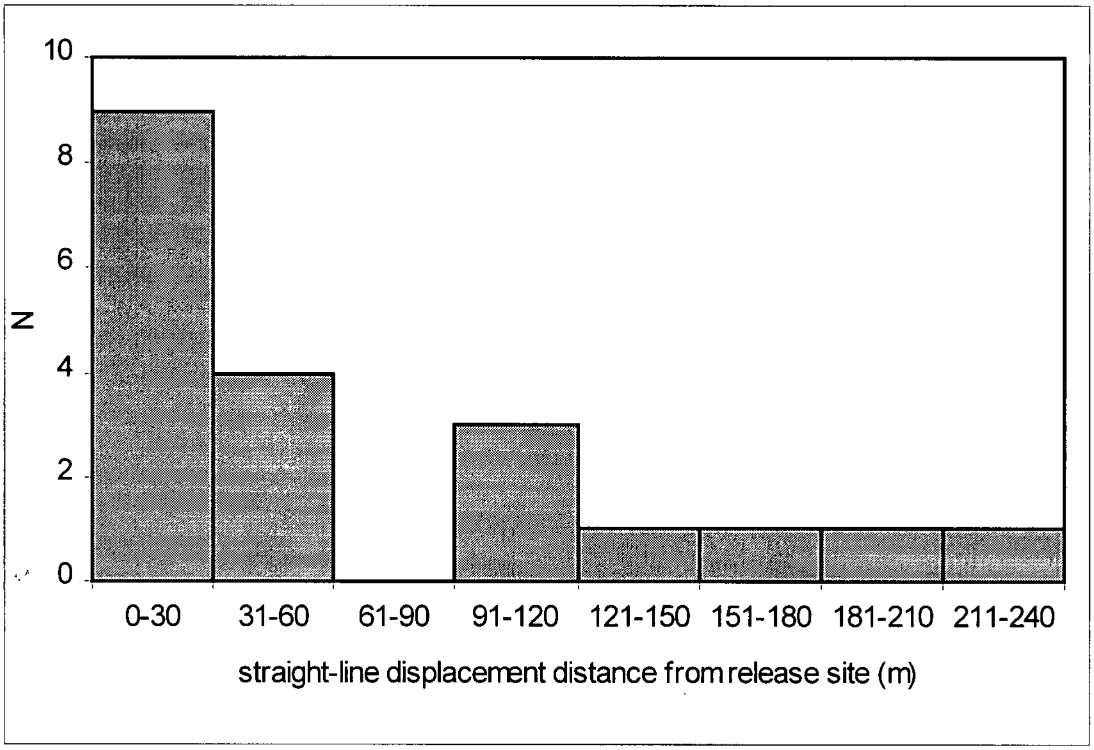

Figure 3.12. Frequency histogram showing straight-line displacement distance between salamander release site and locations recorded two months after release.

CHAPTER IV

CONCLUSIONS AND RECOMMENDATIONS

The Pacific Giant Salamander is a red-listed species in British Columbia where it is found solely within the Chilliwack River drainage basin. This species is considered threatened in B.C. because of its very restricted geographical range and habitat losses to clearcut logging (Farr 1985, Haycock 1991). Although several studies have been conducted investigating both the ecology of larval PGS and the impacts of forestry on the larval stage of this species (e.g. Nussbaum and Clothier 1973, Jones *et al.* 1990, Parker 1991,1994), virtually nothing is known about the secretive terrestrial life stage. The gap in knowledge about this life stage is critical since PGS are believed to live up to 15 or 20 years after they metamorphose. The purpose of my study was to gather information about terrestrial PGS so that this species could be more effectively managed for in the face of habitat loss and alteration. I had four study objectives: (1) to fill in some gaps in the natural history knowledge of terrestrial Pacific Giant Salamanders in British Columbia, particularly with respect to activity patterns and habitat use, (2) to determine the effects of clearcut logging on terrestrial PGS in B.C., (3) to assess the efficacy of riparian buffer strips in maintaining populations of terrestrial PGS in the face of clearcut logging, and (4) to assess the dispersal or recolonization capability of the terrestrial life stage of PGS.

Results of this study indicated that terrestrial PGS were relatively sedentary creatures that tended to move very little despite their capability to do so. There was no evidence to suggest that they defended territories. In fact, they did not appear to occupy restricted home ranges. They wandered somewhat randomly throughout suitable habitat, travelling between the refugia in which they spent the vast majority of their time. They generally sought refuge in or under logs, under rocks, in underground burrows, and in streams. Selection of microsites appeared to be determined in part by the availability of coarse woody debris, water, rock and leaf litter. When using coarse woody debris as refugia, terrestrial PGS selected for wood in advanced stages of decay. The activity level of these salamanders was strongly associated with climatic conditions, particularly rain. They were much more likely to move when it was raining, or had done so in the recent past, than when the weather was dry. In the absence of rain, the salamanders were more active when temperatures were cool, likely because this caused dew to form on the forest floor. Terrestrial PGS were more active at night than during the day. This presumably reduced their risk of desiccation and potentially the risk of predation. They were also more active during the cool, wet fall than during the hot, dry summer. During the study period (summer and fall), there was no evidence to suggest any seasonal migrations either to and from, or up and down the stream.

The response of terrestrial PGS to forest practices was ambiguous. Small sample sizes resulted in very low power to detect differences between the activity of animals tracked in different habitat types. While many study results indicated no difference between the behaviour of salamanders tracked in the different habitat types, several subtle differences were found between clearcut and forested areas. These minor differences suggested that terrestrial PGS may be adversely affected by clearcut logging. Although these very hardy animals appeared capable of surviving in clearcut habitat, catch per unit effort data suggested that their relative abundance was lower there than in forested areas. Animals that inhabited clearcuts also appeared to adjust their behaviour in ways that reduced their risk of desiccation. For example, they remained in their refuges for longer periods of time, and their movements were more strongly associated with precipitation and with season. These behavioural adjustments could detrimentally affect the fitness of animals found in clearcuts if their abilities to find food or mates are compromised. When terrestrial PGS encountered clearcuts, they avoided entering this habitat. As a result, the forest edge acted somewhat as a reflective barrier to salamander movements out of forested stands. This could have serious implications for the dispersal of this species between adjacent streams. Even for animals found in forested habitat, the dispersal probability of terrestrial PGS was quite low (a maximum probability of one in a thousand of an animal travelling from one stream to a neighbouring stream 500 m away during a two-month period of activity). Since clearcuts appear to deflect terrestrial PGS movements, habitat fragmentation caused by clearcut logging would likely further compromise the already low dispersal rates of this species. This could cause problems by interrupting gene flow between neighbouring populations and by greatly decreasing the chance that a locally extirpated area would be recolonized by dispersing terrestrial animals.

Riparian buffer strips appeared to be a promising management strategy for the conservation of terrestrial PGS. Not only do they protect the stream (e.g. Budd *et al.* 1987) and therefore the larval PGS life stage, but they appeared to maintain the relative abundance of terrestrial animals at levels comparable to those in forested habitat. In addition, the movement patterns of terrestrial animals in riparian buffer strips were indistinguishable from those of animals found in continuous forests. The edge created at the boundary of buffer strips, however, may still represent a reflective barrier to terrestrial PGS movements, thereby causing problems for inter-stream dispersal.

In light of this new information about the natural history of the terrestrial PGS and its response to forestry practices, I propose two management alternatives. The first strategy involves maintaining riparian buffer strips of at least 20 m in width along streams known to harbour Pacific Giant Salamanders (Figure 4.1a). This would likely protect both larval and terrestrial animals at these sites. This strategy is consistent with that proposed in a draft copy of the *Managing for Identified Wildlife* Pacific Giant Salamander species account. There are two drawbacks associated with this strategy. First, narrow, linear buffer strips are prone to blowdown. In some instances this effectively results in the destruction of riparian habitat which the buffers were intended to protect (Steinblums *et al*. 1984). Second, the potential barrier to inter-stream dispersal associated with clearcut habitat between neighbouring streams is not addressed by this strategy. If the salamander population at a stream becomes extirpated, either through logging practices or natural events such as stream drying, it will likely be a very long time before this stream is recolonized. A possible solution to this problem is a reintroduction program targeting these locally extirpated streams.

The second management alternatives involves reserve patches rather than riparian buffer strips. These reserve patches, analogous to the Wildlife Habitat Areas (WHAs) outlined in the B.C. Forest Practices Code, would be centred along reaches of headwater streams known to be inhabited by PGS. Some of these patches would also extend across upland forested habitat to adjacent headwater streams (Figure 4.1b). With this management alternative, entire stream channels would not be protected, however, the larger forested reserves would be less susceptible to blowdown than narrow buffers, and the potential for natural inter-stream dispersal would be maintained. A possible drawback of this strategy is that the design may require the construction of more roads and stream crossings in order to access the timber.

In areas where PGS habitat is clearcut, retaining habitat features that provide moisture or shade will likely make the area more hospitable for terrestrial PGS. This includes retaining unmerchantable timber, snags, understorey vegetation, and perhaps most importantly, coarse woody debris. All age classes of coarse wood should be retained to ensure a continual supply of high quality woody debris in advanced stages of decay while the forest regenerates. The retention of such habitat features may enable terrestrial PGS to survive in clearcut areas until the forest canopy is re-established.

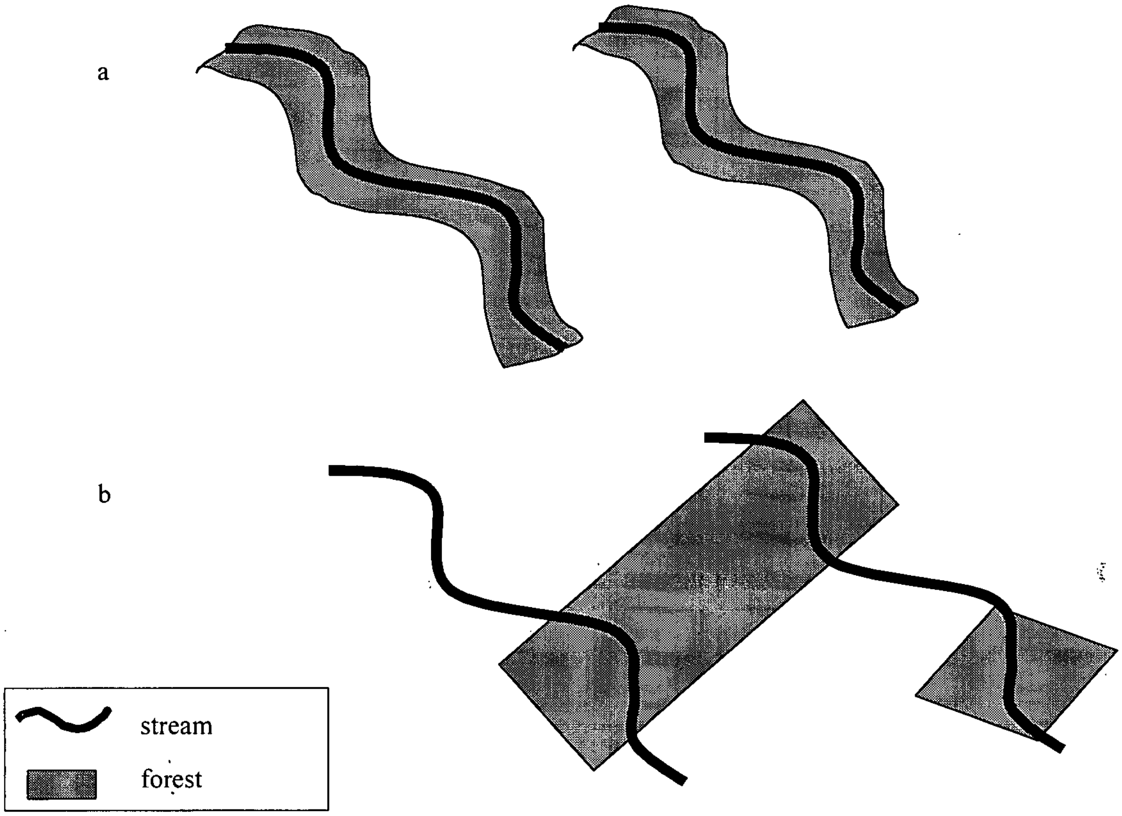

Figure 4.1. Schematic representation of two alternative management strategies for Pacific Giant Salamanders: (a) riparian buffer strips along the length of streams known to be inhabited by PGS, and (b) forested reserves at designated areas along streams and adjoining adjacent streams.

LITERATURE CITED

Ash, A.N. 1988. Disappearance of salamanders from clearcut plots. The Journal of the Elisha Mitchell Scientific Society 104: 116-122.

Ashton, R.E., Jr. 1975. A study of movement, home range, and winter behavior of *Desmognathus fuscus* (Rafinesque). J. Herpetol. 9: 85-91.

Aubry, K.B. and P.A. Hall. 1991. Terrestrial amphibian communities in the southern Washington Cascade range. Pages 327-338 in K.B. Aubry, A.B. Carey, and M.H. Juff (eds.) Wildlife and Vegetation of Unmanaged Douglas-fir Forests. PNW-GTR-285. U.S.D.A. Forest Service, Pacific Northwest Research Station, Portland, Oregon.

Bartels, R., J.D. Dell, R.L. Knight and G. Schaefer. 1985. Dead and down woody material. Pages 171-185 *In* Management of Wildlife and Fish Habitats in Forests of Western Oregon and Washington. Part 1 – Chapter Narratives. USDA Forest Sevice, Pacific Northwest Region, Portland, OR.

Batschelet, E. 1991. Circular Statistics in Biology. New York. Academic Press

B.C. Ministry of Environment and B.C. Ministry of Forests. 1995. Riparian Management Area Guidebook, December 1995.

B.C. Ministry of Environment, Lands and Parks. 1993. Pacific Giant Salamander. Wildlife in British Columbia at Risk Brochure.

Beschta, R.L., R.E. Bibly, G.W. Grown, L.B. Holtby and T.D. Hofstra. 1987. Stream temperature and aquatic habitat: fisheries and forestry interactions. Pages 191-232 *In* Salo, E.O. and T.W. Cundy (eds.). Streamside Management: Forestry and Fishery Interactions. Contrib. 57, Inst. For. Resour., Univ. of Washington, Seattle, WA.

Bisson, P.A., R.E. Bilby, M.D. Bryant, C.A. Dolloff, G.B. Grette, R.A. House, M.L. Murphy, K.V. Koski and J.R. Sedell. 1987. Large woody debris in forested streams in the Pacific Northwest: past, present, and future. Pages 143-190 *In* Salo, E.O. and T.W. Cundy (eds.). Streamside Management: Forestry and Fishery Interactions. Contrib. 57, Inst. For. Resour., Univ. of Washington, Seattle, WA.

Blaustein, A.R. and D.B. Wake. 1995. The puzzle of declining amphibian populations. Scientific American April 1995: 52-57.

Blaustein, A.R., D.B. Wake and W.P. Sousa. 1994. Amphibian declines: judging stability, persistence, and susceptibility of populations to local and global extinctions. Cons. Biol. 8: 60-71.

Blaustein, A.R., J.J. Beatty, D.H. Olson and R.M. Storm. 1995. The Biology of Amphibians and Reptiles in Old-growth Forests in the Pacific Northwest. Gen. Tech.

Rep. PNW-GTR-337. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Bren, L.J. 1995. Aspects of the geometry of riparian buffer strips and its significance to forestry operations. Forest Ecology and Management 75: 1-10.

Brosofske, K.D., J. Chen, R.J. Naiman and J.F. Franklin. 1997. Harvesting effects on microclimatic gradients from small streams to uplands in western Washington. Ecological Applications 7:1188-1200.

Brown, G.W. and J.T. Krygier. 1970. Effects of clearcutting on stream temperature. Water Resour. Res. 6:1133-1139.

Budd, W.W., P.L. Cohen, P.R. Saunders, and F.R. Steiner. 1987. Stream corridor management in the Pacific Northwest: I. Determination of stream-corridor widths. Environ. Manage. 11: 587-597.

Bury, R.B. 1983. Differences in amphibian populations in logged and old growth redwood forest. Nothwest Science 57: 167-178.

Bury, R.B., P.S. Corn, and K.B. Aubry. 1991. Regional patterns of terrestrial amphibian communities in Oregon and Washington. Pages 341-350 *In* K.B. Aubry, A.B. Carey, and M.H. Juff (eds.) Wildlife and Vegetation of Unmanaged Douglas-fir Forests. PNW-GTR-285. U.S.D.A. Forest Service, Pacific Northwest Research Station, Portland, Oregon.

CALHOME (California HOMErange). Kie, J.G., J.A. Baldwin, and C.J. Evans. 1994. U.S. Forest Service, Pacific Southwest Research Station.

Capen, D.E., J.W. Fenwick, D.B. Inkley, and A.C. Boynton. 1986. Multivariate models of songbird habitat in New England forests. Pages 171-182 *In* J. Verner., M.L. Morrison, and C.J. Ralph, eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Univ. Wisconsin Press, Madison.

Chen, J., J.F. Franklin, and T.S. Spies. 1993. Contrasting microclimates among clearcut, edge, and interior old-growth Douglas-fir forest. Agri. For. Metero. 63: 219-237.

Chen, J., J.F. Franklin, and T.S. Spies. 1995. Growing season microclimatic gradients from clearcut edges into old-growth Douglas-fir forest. Ecological Applications 5: 74-86.

Conner, E.J., W.J. Trush and A.W. Knight. 1988. Effects of logging on Pacific Giant Salamanders: influence of age-class composition and habitat complexity. Bull. Ecol. Soc. of Am. 69(suppl.): 104-105.

Corn, P.S. and R.B. Bury. 1989. Logging in western Oregon: responses of headwater habitats and stream amphibians. For. Ecol. and Manage. 29: 39-57.

Cross, S.P. 1985. Responses of small mammals to forest riparian perturbations. Pages 269-275 *In* Riparian Ecosystems and Their management: Reconciling Conflicts in Use., Tuscon, AR.

Davies, P.E. and M. Nelson. 1994. Relationships between riparian buffer widths and the effects of logging on stream habitat, invertebrate community composition and fish abundance. Aust. J. Mar. Freshwater Res. 45: 1289-1305.

Dethlefsen, E.S. 1948. A subterranean nest of the Pacific Giant Salamander, *Dicamptodon ensatus* (Eschscholtz). Wasmann Collector 7: 81-84.

Dice, L.R. 1952. Natural Communities. University of Michigan Press, Ann Arbor.

Diefenbach, D.R. and R.B. Owen Jr. 1989. A model of habitat use by breeding American black ducks. J. Wildl. Manage. 53: 383-389.

Diller, J.S. 1907. A salamander – snake fight. Science:XXVI: 907-908.

Duellman, W.E. and L. Trueb. 1986. Biology of Amphibians. McGraw-Hill, New York.

Dupuis, L.A. 1993. The Status and Distibution of Terrestial Amphibians in Old-growth Forests and Managed Stands. M.Sc. Thesis, University of British Columbia, Vancouver, B.C.

Dupuis, L.A., J.N. Smith, and F. Bunnell. 1995. Relation of terrestial-breeding amphibian abundance to tree-stand age. Conservation Biology 9: 645-653.

Enge, K.M. and W.R. Marion. 1986. Effects of clearcutting and site preparation on herpetofauna of north Florida flatwoods. For. Ecol. and Manage. 14: 177-192.

Farr, A.C.M. 1985. Status report on the Pacific Giant Salamander (*Dicamptodon ensatus*) in Canada – 1985. Unpublished report to the B.C. Ministry of Environment, Wildlife Branch.

Feder, M.E. 1983. Integrating the ecology and physiology of plethodontid slamanders. Herpetologica 39: 291-310.

Fitch, H.S. and P.L. von Achen. 1977. Spatial relationship and seasonality in the skinks *Eumeces fasciatus* and *Scincella laterale* in northeastern Kansas. Herpetologica 33: 303-313.

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

Gascon, C. 1993. Breeding-habitat use by five Amazonian frogs at forest edge. Biodiversity and Conservation 2: 438-444.

Good, D.A. 1989. Hybridization and cryptic species in *Dicamptodon* (Caudata: Dicamptodontidae). Evolution 43: 728-744.

Graf, W. 1949. Observations on the salamander *Dicamptodon.* Copeia 1949: 79-80.

Hall, J.D., M.L. Murphy and R.S. Aho. 1978. An improved design for assessing impacts of watershed practices on small streams. Verh. Internat. Verein. Limnol. 20: 1359-1365.

Harris, J.P. 1981. Intrapond homing behavior in *Notophthalmus viridescens.* J. of Herpetology 15: 355-356.

Harris, S., W.J. Cresswell, P.G. Forde, WlJ. Trewhella, T. Woollard, and S. Wray. 1990. Home-range analysis using radio-tracking data – a review of problems and techniques particularly as applied to the study of mammals. Mammal Rev. 20: 97-123.

Hartman, G., J.C. Scrivener, L.B. Holtby and L. Powell. 1987. Some effects of different streamside treatments on physical conditions and fish population processes in Carnation Creek, a coastal rain forest stream in British Columbia. Pages 330-372 *In* Salo, E.O. and T.W. Cundy (eds.). Streamside Management: Forestry and Fishery Interactions. Contrib. 57, Inst. For. Resour., Univ. of Washington, Seattle, WA.

Haycock, R.D. 1991. Pacific Giant Salamander *Dicamptodon tenebrosus* Status Report. Unpublished report to the B.C. Ministry of Environment, Wildlife Branch.

Hays, W.L. 1988. Statistics, 4th edition. Holt, Rinehart and Winston, New York.

Healy, W.R. 1975. Terrestrial activity and home range in efts of *Notophthalmus viridescens.* The Amer. Midl. Nat. 93: 131-138.

Henry, W.V. and V.C. Twitty. 1940. Contributions to the life histories of *Dicamptodon ensatus* and *Ambystoma gracile.* Copeia 1940: 247-250.

Horn, H.S. 1983. Some theories about dispersal. Pages 54-62 *In* Swingland, I.R. and P.J. Greenwood (eds.). The Ecology of Animal Movement. Clarendon Press, Oxford.

Hutchinson, V. 1961. Critical thermal maxima in salamanders. Physiol. Zool. 34: 92-125.

Jaeger, R.G. 1980a. Microhabitats of a terrestrial forest salamander. Copeia 1980: 265-268.

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

Johnson, B. 1992. Habitat loss and declining amphibian populations. *In* Bishop, C.A. and K.E. Pettit (eds.). Declines in Canadian Amphibian Populations: Designing a National Monitoring Strategy. Occasional Paper #76, Canadian Wildlife Service.

Jones, L.L.C, R.B. Bury and P.S. Corn. 1990. Field observation of the development of a clutch of Pacific Giant Salamander (*Dicamptodon tenebrosus*) eggs. Northwestern Naturalist 71: 93-94.

Kelsey, K.A. 1995. Responses of Headwater Stream Amphibians to Forest Practices in Western Washington. Ph.D. Dissertation, University of Washington, Seattle, WA.

Kessel, E.L, and B.B. Kessel. 1944. Metamorphosis of the Pacific giant salamander, *Dicamptodon ensatus* (Eschscholtz). Wasmann Collector 6: 38-48.

Kinley, T. and N. Newhouse. 1995. Riparian reserve strips and wildlife: Invermere Forest District. Silviculture Systems Wildlife Habitat Research and Extension, Research Update SS058, B.C. <in. of Env. and B.C. Min. of For., Victoria.

Kleeberger, S.R. and J.K. Werner. 1982. Home range and homing behavior of *Plethodon cinereus* in northern Michigan. Copeia 1982: 409-415.

Krajina, V.J. 1965. Biogeoclimatic zones and classification of British Columbia. Ecol. Western N. Amer. 1: 1-17.

Kramer, P., N. Reichenbach, M. Hayslett, and P. Sattler. 1993. Population dynamics and conservation of the Peaks of Otter Salamander, *Plethodon hubrichti*. J. of Herpetology 27: 431-435.

Leonard, W.P., H.A. Brown, L.L.C. Jones, D.R. McAllister and R.M. Storm. 1993. Amphibians of Washington and Oregon. Audubon Society, Seattle, WA.

Loredo, I, D. Van Vuren and M.L. Morrison. 1996. Habitat use and migration behavior of the California Tiger Salamander. J. of Herpetology 30: 282-285.

Lovejoy, T.E. R.O. Bierregaard Jr., A.B. Rylands, J.R. Malcolm,C.E. Quintela, L.H. Harper, K.S. Brown Jr., A.H. Powell, G.V.N. Powell, H.O.R. Schubart and M.B. Hays. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257-285 In Soulé, M.E. (ed.) Conservation Biology. The Science of Scarcity and Diversity. Sinauer Associates Inc., Sunderland, Mass.

MacDonald D.W., F.G. Ball and N.G. Hough. 1980. The evaluation of home range size and configuration using radiotracking data. Pages 405-424 *In* C.J. Amlander and D.W.

MacDonald (eds.). A Handbook on Biotelemetry and Radio Tracking. Pergamon Press, Oxford, U.K.

Madison, D.M. 1997. The emigration of radio-implanted Spotted Salamanders, *Ambystoma maculatum*. Journal of Herpetology 31: 542-551.

Maiorana, V.C. 1978. Difference in diet as an epiphenomenon: space regulates salamanders. Can. J. Zool. 56: 1017-1025.

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

Morrison, M.L., W.M. Block, L.S. Hall, and H.S. Stone. 1995. Habitat characteristics and monitoring of amphibians and reptiles in the Huachuca Mountains, Arizona. The Southwestern Naturalist 40: 185-192.

Murphy, M.L. and J.D. Hall. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Can. J. Fish. Aquat. Sci. 38: 137-145.

Murphy, M.L., J. Heifetz, S.W. Johnson, K.W. Koski, and J.K. Thedinga. 1986. Effects of clear-cut logging with and without buffer strips on juvenile salmonids in Alaskan streams. Can. J. Fish. Aquat. Sci. 43: 1521-1533.

Newbold, J.D., D.C. Erman, and K.B. Roby. 1980. Effects of logging on macroinvertebrates in streams with and without buffer strips. Can. J. Fish. Aquat. Sci. 37:1076-1085.

Nussbaum, R.A. 1969. Nests and eggs of the Pacific Giant Salamander, *Dicamptodon ensatus* (Eschscholtz). Herpetologica 25: 257-262.

Nussbaum, R.A. and G.W. Clothier. 1973. Population structure, growth, and size of larval *Dicamptodon ensatus* (Eschscholtz). Northwest Science 47: 218-227.

Nussbaum, R.A., E.D. Brodie, Jr. and R.M. Storm. 1983. Amphibians and Reptiles of the Pacific Northwest. The University of Idaho Press, Moscow.

O'Llaughlin, J. and G.H. Belt. 1994. Functional approaches to riparian buffer strip design. J. of Forestry Feb. 1995: 29-32.

Packer, W.C. 1960. Bioclimatic influences on the breeding migration of *Taricha rivularis*. Ecology 41: 509-517.

Palis, J.G. 1997. Breeding migration of *Ambystoma cingulatum* in Florida. J. of Herpetology 31: 71-78.

Parker, M.S. 1991. Relationship between cover availability and larval Pacific Giant Salamander density. J. of Herpetology 25: 355-357.

Parker, M.S. 1994. Feeding ecology of stream-dwelling Pacific Giant Salamander larvae (*Dicamptodon tenebrosus*). Copeia 1994: 705-718.

Parmelee, J.R. 1993. Microhabitat segregation and spatial relationships among four species of mole salamanders (Genus *Ambystoma*). Occasional Papers of the Museum of Natual History, the Univesity of Kansas 160: 1-33.

Pechmann, J.H.K., D.E. Scott, R.D. Semlitsch, J.P. Caldwell, L.J. Vitt and J.W Gibbons. 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. Science 253: 892-895.

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

Phillips, K. 1990. Where have all the frogs and toads gone? BioScience 40: 422-424.

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

Ray, C. 1958. Vital limits and rates of desiccation in salamanders. Ecology 39: 75-83.

Richardson, J.S. and W.E. Neill 1995. Distribution patterns of two montane stream amphibians and the effects of forest harvest: the Pacific Giant Salamander and Tailed Frog in southwestern British Columbia. Unpublished Report to the British Columbia Ministry of Environment, Lands and Parks.

Rosenberg, K.V. and M.G. Raphael. 1986. Effects of forest fragmentation on vertebrates in Douglas Fir Forests. Pages 263-272 *In* Verner, J., M.L. Morrison and C.J. Ralph. Wildlife 2000. Modeling Habitat Relationships of Terrestrial Vertebrates. University of Wisconsin Press, Madison.

Savage, J.M. 1960. Evolution of peninsular herpetofauna. Syst. Zool. 9:184-212.

Schoener, J.R. 1981. An empirically based estimate of home range. Theor. Pop. Bio. 20: 281-325.

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

Semlitsch, R.D. 1985. Analysis of climatic factors influencing migrations of the salamander *Ambystoma talpoideum*. Copeia 1985: 477-489.

Semlitsch, R.D. and J.H.K. Pechmann. 1985. Diel pattern of migratory activity for several species of pond-breeding salamanders. Copeia 1985: 86-91.

Sharma, S. 1996. Applied Multivariate Techniques. John Wiley and Sons, Inc. New York.

Sinsch, U. 1990. Migration and orientation in anuran amphibians. Ethology Ecology and Evolution 2: 65-79.

Sjogren, P. 1991. Extinction and isolation gradients in metapopulations: The case of the pool frog (*Rana lessonae*). Biol. J. Linn. Soc. 42: 135-147.

Spotila, J.R. 1972. Role of temperature and water in the ecology of lungless salamanders. Ecol. Monogr. 42: 95-125.

Staub, N.L., C.W. Brown and D.B. Wake. 1995. Patterns of growth and movements in a population of *Ensatina eschscholtzii platensis* (Caudata: Plethodontidae) in Sierra Nevada, California. J. of Herpetology 29: 593-599.

Steinblums, I.J., H.A. Fooehlich and J.K. Lyons. 1984. Designing stable buffer strips for stream protection. J. of Forestry Jan. 1984: 49-52.

Steventon, D., L. Dupuis and R. Friele. 1996. Riparian management and the Tailed Frog in northern coastal forests. Extension Note # 15, Forest Sciences, Prince Rupert Forest Region, Forest Service British Columbia.

Tabachnick, BG and LS Fidell. 1996. Using Multivariate Statistics, 3rd edition. Harper Collins College Publishers, New York.

Triquet, A.M., G.A. McPeek and W.C. McComb. 1990. Songbird diversity in clearcuts with and without riparian buffer strip. J. Of Soil and Water Cons. July-August 1990: 500-503.

Triska, F.J. and K. Cromack, Jr. 1979. The role of wood debris in forests and streams. Pages 171-189 *In* Forests: Fresth Perspectives from Ecosystem Analysis. Proceedings of the 4th Annual Biology Colloquium. Corvalis State University Press.

Vesely, D.G. 1996. Terrestrial Amphibian Abundance and Species Richness in Headwater Riparian Buffer Strips, Oregon Coast Range. M.Sc. Thesis, Oregon State University, Corvallis.

Wahbe, T.R. 1996. Tailed Frogs (*Ascaphus truei*, Stejneger) in Natural and Managed Coastal Temperate Rainforests of Southwestern British Columbia, Canada. M.Sc. Thesis, University of British Columbia, Vancouver, B.C.

Wells, K.D. 1980. Spatial associations among individuals in a population of Slimy salamanders (*Plethodon glutinosus*). Herpetologica 36: 271-275.

Welsh, H.H. Jr. 1990. Relictual amphibians and old-growth forests. Cons. Biol. 4: 309-319.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70: 164-168.

Yahner, R.H. 1988. Changes in wildlife communities near edges. Cons. Bio. 2: 333-339.

Zar, J..H. 1984. Biostatistical Analysis, 2nd edition. Prentice Hall, Englewood Cliffs, New Jersey.

Zug, G.R. 1993. Herpetology. An Introductory Biology of Amphibians and Reptiles. Academic Press, Inc., San Diego, CA.