

**COEUR D'ALENE SALAMANDER ABUNDANCE, DISTRIBUTION, AND
HABITAT USE IN MOUNT REVELSTOKE NATIONAL PARK OF CANADA**

by

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ABSTRACT

The Coeur d'Alene salamander (*Plethodon idahoensis*) is a species of special concern throughout its global range, which includes southeastern BC (COSEWIC, Nov 2007), Idaho, and Montana, due to disjunct populations and sensitivity to human disturbance. Within the Interior Cedar-Hemlock forest on Mount Revelstoke, BC, Coeur d'Alene salamanders occur at their highest abundance between 600 m and 800 m. Beyond the Mount Revelstoke National Park boundaries, the low-order stream habitat of this species is subject to disturbance from forestry, mining, road building, road maintenance, and watercourse diversions such as run-of-the-river hydro projects.

We conducted nocturnal salamander surveys and assessed habitat characteristics on 12 Sites (750 m² – 1000 m² stream transects) along three streams from June through September 2006. Coeur d'Alene salamanders were detected from 600 m - 1000 m on seven of the 12 study sites. Relative abundance of Coeur d'Alene salamanders ranged from 0.005 ± 0.001 per m² to 0.025 ± 0.005 per m² on six sites below 950 m. Coeur d'Alene salamanders occurred at an average of 0.001 ± 0.001 per m² at 972 m, the only site above 950 m where we detected salamanders. Our capture-mark-recapture efforts of three surveys per month in June and August yielded a very low recapture rate (3.95 %). Coeur d'Alene salamanders are challenging to enumerate due to their vertical distribution within the soil and underlying geological material.

Neonate, juvenile, and adult Coeur d'Alene salamanders were observed from June to September and the highest proportion of neonates occurred in June, soon after the salamanders emerged from winter hibernation. Results of a logistic regression analysis of 1-m² plots reflected the importance of fine scale habitat characteristics (quadrat gradient,

boulder, cobble, moss, grass, and shrub) in addition to site-level habitat features (water volume and elevation) that in combination describe the association of Coeur d'Alene salamanders with cool and moist conditions. Coeur d'Alene salamanders appear to select streambed habitat during warm, dry periods, which may be a behavioural response to minimize dehydration during periods of activity at the surface of the forest floor.

TABLE OF CONTENTS

ABSTRACT	ii
TABLE OF CONTENTS	iv
LIST OF TABLES	vi
LIST OF FIGURES	viii
ACKNOWLEDGEMENTS	xi
1 INTRODUCTION	1
1.1 NATURAL HISTORY	4
1.2 HABITAT ASSOCIATIONS	5
1.3 STATUS OF <i>PLETHODON IDAHOENSIS</i>	6
2 MATERIALS AND METHODS	8
2.1 STUDY AREA AND SITE SELECTION	8
2.2 SALAMANDER SURVEYS	12
2.3 HABITAT DATA	16
2.4 STATISTICAL ANALYSES	19
2.4.1 <i>Habitat description</i>	20
2.4.2 <i>Microhabitat associations</i>	21
3 RESULTS	23
3.1 SALAMANDER RELATIVE ABUNDANCE	23
3.2 AGE STRUCTURE	25
3.3 DISTRIBUTION	29
3.4 HABITAT DESCRIPTION	32
3.4.1 <i>Stream habitat</i>	32
3.4.2 <i>Terrestrial habitat</i>	35
3.4.3 <i>Microhabitat associations</i>	37
3.4.3.1 <i>Stream habitat</i>	37
3.4.3.2 <i>Terrestrial habitat</i>	39

4 DISCUSSION 41
 4.1 SALAMANDER RELATIVE ABUNDANCE..... 41
 4.2 SPATIAL DISTRIBUTION..... 43
 4.2.1 Site level distribution..... 44
 4.3 HABITAT..... 46
 4.3.1 Microhabitat..... 46
 4.4 FUTURE RESEARCH 48
5 CONCLUSION..... 50
WORKS CITED..... 51
APPENDIX: Coordinates of Coeur d’Alene salamander survey locations 59

LIST OF TABLES

Table 2.1: Continuous variables were used in exploratory factor analysis of stream and terrestrial habitat up to 5 m beyond stream centre on seven study sites in Mount Revelstoke National Park, Canada. Data were collected on seven sites on three streams where Coeur d’Alene salamanders were detected during the summer of 2006. Continuous (Con) and categorical (Cat) variables were considered for logistic regression (LR) analysis. LR was applied to investigate the relationship between the habitat characteristics of used and available 1-m ² quadrats along streams inhabited by Coeur d’Alene salamanders.....	17
Table 2.2: Continuous variables (mean ± 1 SE) used in the site level habitat description factor analysis, stratified by habitat type (streambed and terrestrial).	21
Table 3.1: Monthly variation in Coeur d’Alene salamander life stage proportions from June to September 2006 on site MON2. Life stages were based on snout-vent-length categories following Lynch (1984). Salamander captures on MON2 were summed across three surveys per month. The mean salamanders of six sites was estimated from three surveys of two sites on each of three streams (abbreviated MON, 5KB, and DBF) in June and repeated in August of 2006 on Mount Revelstoke, B.C.....	28
Table 3.2: Three factor model resulting from exploratory factor analysis of stream habitat variables that describe Coeur d’Alene salamander habitat along streams on Mount Revelstoke, BC. Values represent the correlations between variables and the explanatory factor, also called factor loadings. Bold values indicate the variables that load primarily on a single Factor, from which the factor descriptor (in parentheses) is derived.....	32
Table 3.3: Two factor model resulting from exploratory factor analysis of stream habitat variables that describe Coeur d’Alene salamander habitat along streams on Mount Revelstoke, BC. Values represent the correlations between variables and the explanatory factor, also called factor loadings. Bold values indicate the variables that load primarily on a single factor, from which the factor descriptor (in parentheses) is derived.....	33
Table 3.4: Three factor model resulting from exploratory factor analysis of terrestrial habitat variables that describe Coeur d’Alene salamander habitat along streams on Mount Revelstoke, BC. Values represent the correlation between each variable and each factor, also called factor loadings. Bold values indicate the variables that load primarily on a single factor, from which the factor descriptor (in parentheses) is derived.....	36

Table 3.5: Candidate models of Coeur d'Alene salamander stream microhabitat associations from logistic regression analysis. Stream variables were initially retained by the stepwise procedure using PROC LOGISTIC in SAS. Further fitting of the models required removal of variables based on maximum likelihood estimates > 0.05 . AIC_c are Akaike units corrected for small sample size, $-2LL$ is the -2 log likelihood, K is the number of parameters and n is the number of observations. Models are sorted by AIC_c 38

Table 3.6: Candidate models of Coeur d'Alene salamander terrestrial microhabitat associations from logistic regression analysis. Terrestrial variables were initially retained by the stepwise procedure using PROC LOGISTIC in SAS. Further fitting of the models required removal of variables based on maximum likelihood estimates > 0.05 . AIC_c are Akaike units corrected for small sample size, $-2LL$ is the -2 log likelihood, K is the number of parameters and n is the number of observations. Models are sorted by AIC_c 40

LIST OF FIGURES

- Figure 2.1: Map of the study area centered on Mount Revelstoke National Park of Canada. The area ranges from 450 m to 1400 m on the southwest facing slope of Mount Revelstoke, BC. Mount Revelstoke is located in the southeast corner of British Columbia (Inset). Study sites where salamanders were detected are indicated with black circles and study sites where no salamanders were detected over repeated surveys are indicated with red triangles. Map provided courtesy of Parks Canada..... 11
- Figure 2.2: (A) Study stream 5KB in Mount Revelstoke National Park, (Black and White photo). (B) Walk-and-turn survey method used during nocturnal visual encounter surveys for Coeur d'Alene salamanders. Sites were 10 m wide centered on the stream and 75-100 m along the stream. (C) Habitat characteristics were measured at salamander capture locations and every 5 m along stream at stream centre (C) and random (R) distances (1-5 m) on either side of the stream. 13
- Figure 3.1: Mean abundance of Coeur d'Alene salamanders (± 1 SE) estimated from three nocturnal visual encounter surveys of each site in Mount Revelstoke National Park during August 2006. Three surveys were conducted on four sites (1-4) on each of three streams (abbreviated 5KB, DBF, and MON). 23
- Figure 3.2: Mean abundance of Coeur d'Alene salamanders (± 1 SE) estimated from three nocturnal visual encounter surveys of six study sites accessible both in June and in August 2006. Visual encounter surveys were conducted after dark on two sites per stream (abbreviated 5KB, DBF, and MON) in Mount Revelstoke National Park..... 24
- Figure 3.3: Mean abundance of Coeur d'Alene salamanders (± 1 SE) averaged across four sites per stream (abbreviated 5KB, DBF, and MON) during August 2006 on Mount Revelstoke, BC. Abundance was estimated from the sum of salamanders captured during three visual encounter surveys of each site standardized by area searched. In each elevation stratum (Low < 950 m < High), mean salamander abundance was estimated across six sites, two sites per stream (5KB, DBF, and MON). 25
- Figure 3.4: Size-class distribution of Coeur d'Alene salamanders on Mount Revelstoke, BC in June and August 2006. Visual encounter survey observations were summed across three surveys of six sites, two sites on each of three streams, in June and repeated in August 2006. Life stages followed Lynch (1984). 26

Figure 3.5:	The proportions of juvenile and adult Coeur d’Alene salamanders on three streams on Mount Revelstoke, BC in June 2006. Proportions are based on total salamanders captured over three visual encounter surveys of two sites (below 950 m) per stream (abbreviated 5KB, DBF, and MON) in June 2006. .	27
Figure 3.6:	The proportions of juvenile and adult Coeur d’Alene salamanders on three streams on Mount Revelstoke, BC in August 2006. Proportions are based on total salamanders captured over three visual encounter surveys of two sites (below 950 m) per stream (abbreviated 5KB, DBF, and MON) in August 2006.....	27
Figure 3.7:	Mean abundance of juvenile and adult Coeur d’Alene salamanders estimated from three nocturnal visual encounter surveys per month (June – September 2006) of site MON2 in Mount Revelstoke National Park, Canada.....	28
Figure 3.8:	Distribution of Coeur d’Alene salamander captures by distance to surface water during nocturnal visual encounter surveys from June through September 2006 on Mount Revelstoke, BC. Distance from the salamander capture location to the nearest standing water pool or stream flow was recorded at the time of capture.....	29
Figure 3.9:	Mean proportion of Coeur d’Alene salamanders (+ 1 SE) captured in stream and terrestrial habitat during three surveys in June 2006 and August 2006 on Mount Revelstoke. Mean proportion was estimated across six sites below 950 m, two sites on each of three streams. The average proportion of stream and terrestrial habitat available across the six sites surveyed is displayed in the far right column.....	30
Figure 3.10:	Mean proportion of adult and juvenile Coeur d’Alene salamanders (+ 1 SE) captured in stream and terrestrial habitat on Mount Revelstoke in June and August 2006. Mean proportion of stream and terrestrial habitat used by each life stage in June and August 2006 was estimated across six sites below 950 m, two sites on each of three streams. The average proportion of stream and terrestrial habitat available across the six sites surveyed is displayed in the far right column.	31
Figure 3.11:	Mean proportion (+ 1 SE) of Coeur d’Alene salamanders within stream habitat on Mount Revelstoke, BC in June and August 2006 relative to the average air temperature during the surveys. Mean proportion was estimated across six sites below 950 m, two sites per stream. The average air temperature was estimated from measurements taken at the beginning of each visual encounter survey. Visual encounter surveys were conducted on six sites in June and August 2006 and repeated three times per month.....	31

Figure 3.12: Available stream habitat site scores for factor 1 (geomorphology) and factor 2 (surface water) that differentiate habitat characteristics among 12 study sites on Mount Revelstoke, B.C. Factor scores for each site are based on a z-score scale ranging from -3.0 to + 3.0. Sites are coded by catch-per-unit-effort (CPUE), an indicator of relative abundance of Coeur d’Alene salamanders on the study sites in 2006. 34

Figure 3.13: Available stream habitat site scores for factor 2 (surface water) and factor 3 (bank gradient) that differentiate habitat characteristics among 12 study sites on Mount Revelstoke, B.C. Factor scores for each site are based on a z-score scale ranging from -3.0 to + 3.0. Sites are coded by catch-per-unit-effort (CPUE), an indicator of relative abundance of Coeur d’Alene salamanders on the study sites in 2006. 34

Figure 3.14: Available terrestrial habitat site scores for factor 1 (substrate) and factor 2 (ground cover) that differentiate habitat characteristics among 12 study sites on Mount Revelstoke, B.C. Sites are coded by catch-per-unit-effort (CPUE), an indicator of relative abundance of Coeur d’Alene salamanders on the study sites in 2006. Site MON2 scored high on all three substrate variables, gravel, sand, and bare soil. 36

Figure 3.15: Available terrestrial habitat site scores for factor 2 (ground cover) and factor 3 (gradient) that differentiate habitat characteristics among 12 study sites on Mount Revelstoke, B.C. Sites are coded by catch-per-unit-effort (CPUE), an indicator of relative abundance of Coeur d’Alene salamanders on the study sites in 2006 37

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1 INTRODUCTION

Globally, we continue to observe the extinction, extirpation, and decline of wildlife species (International Union for Conservation of Nature and Natural Resources (IUCN) 2007). At the same time, over 6.5 billion people, growing in population at a rate of $> 1\%/yr$ (United Nations 2007) clear forests for agriculture and fuel, dam rivers for hydroelectric power and mine non-renewable resources. As a result, plants, animals, and the ecosystems in which they function are compromised (Foley et al. 2005; Andre et al. 2008; Srinivasan et al. 2008). Species and populations have declined due to habitat degradation, caused by agricultural conversions (Kerr & Cihlar 2004), habitat loss (Becker et al. 2007; Polus et al. 2007), pollution, introduced invasive species (Cambray 2003), disease (Daszak et al. 2003) and climate change (Daszak et al. 2005; Bauer et al. 2008). Climate change has been identified as a factor contributing to the detrimental effects of habitat degradation (Warren et al. 2001; Travis 2003). It is usually difficult to isolate one factor causing the decline of a population. Often, multiple factors are acting together on sensitive species, sometimes with cumulative or synergistic consequences (Opdam & Wascher 2004).

Species conservation is critical when populations are threatened by single or multiple resource uses. Land-use managers are challenged with balancing resource consumption and ensuring the persistence of species and ecosystem processes. The IUCN (2001) classifies species at risk of global extinction as Critically Endangered, Endangered, or Vulnerable. Endangered species are at immediate risk of becoming extinct throughout their entire range or a significant portion of their range. The IUCN (2001) states that “a taxon may require conservation action even if it is not listed as threatened” (p.6).

In Canada, species are assessed for their risk of extinction or extirpation by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (COSEWIC 2006). A particular taxon may be assessed as Threatened or Endangered by COSEWIC (2006) based on biological indicators such as declining population or small distribution with decline or fluctuation. During the assessment process, COSEWIC considers the following population parameters related to the assessment criteria: total population size, observed or potential decline, extent of occurrence, area of occupancy, and the number of mature individuals in the population (COSEWIC 2006). Canada's Species at Risk Act (SARA) defines species of Special Concern as "wildlife species that may become a threatened or an endangered species because of a combination of biological characteristics and identified threats" (Government of Canada 2002). Over 500 species of plants and animals have been assessed by COSEWIC (2007) as at risk of extirpation or extinction in Canada. There are many more species that need to be assessed, or require more data, so conservation plans can be developed as needed. In Canada, the recovery of threatened and endangered species is a nationally coordinated effort relying on federal, provincial, and territorial representatives working together.

Rare or uncommon species may have few or small, isolated populations, or be difficult to detect with casual observation or standard survey methods. Rare species have the greatest need of conservation action to prevent the complete loss of populations to stochastic events. Effective conservation of threatened species requires adequate data on the size, structure, and distribution of populations over time (Giralt & Valera 2007; Tobias & Brightsmith 2007). Not only are adequate data required, but the methods applied in collecting the necessary data must first minimize biases and account for sources of uncertainty (Williams 2001; Thompson 2004). Once appropriate sampling methods are

applied that increase the probability of detecting a rare or elusive species, resource managers will have greater confidence in trend estimates and demographic responses to management actions (Thompson 2004).

Of 25,238 vertebrate species assessed for their risk of global extinction by the IUCN, amphibian species are proportionately more at risk (29%) than either mammals (20%) or birds (12%) (IUCN 2007). The suspected cause of amphibian declines worldwide is the destruction, degradation, and fragmentation of habitat or corridors between habitats, (Smith & Green 2005; Becker et al. 2007; Gardner et al. 2007). Amphibian diversity is threatened across global, regional, and local scales by stochastic and anthropogenic habitat modification including conversion of critical habitat to agriculture. Introduced species, disease (Daszak et al. 2003; Skerratt et al. 2007) and pollutants also threaten the persistence of sensitive species (Duellman & Sweet 1999; Boone et al. 2007). Amphibian conservation is further challenged by observed declines in seemingly pristine habitats (Duellman & Sweet 1999).

Some of Canada's amphibian and reptile populations are declining (Environment Canada 2004). Of 35 native amphibian species evaluated by COSEWIC, 20 have been assessed as threatened, endangered, or have the potential to become threatened or endangered (special concern) due to their sensitivity to habitat degradation (COSEWIC 2007).

Amphibians are particularly threatened by human activities that alter the temperature and moisture conditions within their habitat. In order to protect habitat of adequate quality and extent, managers tasked with balancing species conservation and human resource use first need to determine species' abundance, distribution, habitat associations, and any requirements for specific environmental conditions (Haan et al. 2007).

1.1 NATURAL HISTORY

Recent phylogenetic research supports the hypothesis that the Coeur d'Alene salamander (*Plethodon idahoensis*) and its sister species, Van Dyke's salamander (*P. vandykei*) were separated by a geological or climatological event approximately 3.75 million years ago (Carstens et al. 2004). The Coeur d'Alene salamander has likely dispersed northward from glacial refugia in the Clearwater River drainage of northern Idaho into northwestern Montana and southeastern British Columbia (BC) by as much as 50 m annually (Carstens et al. 2004). As the Cordilleran Ice Sheet retreated northward, this salamander likely dispersed over unconsolidated materials that are now too dry to inhabit. Isolated populations remain along the Columbia River, the Kootenay River, and their tributaries throughout northwestern Montana and southeastern BC. The upper elevation record for the Coeur d'Alene salamander is 1,524 m in Ravalli County, Montana, USA.

Coeur d'Alene salamanders have black or dark brown bodies with silver speckles and a yellow, orange, or red dorsal stripe. The dorsal stripe has irregular edges and is reduced to patches on the head and tip of the tail. Distinguishing features are the irregular shaped patch of yellow or white on the throat and slightly webbed toes (Nussbaum et al. 1983). Coeur d'Alene salamander neonates are 16-22 mm snout-vent-length (SVL), juveniles are 23-43 mm SVL, and adults are 44-60 mm SVL (Lynch 1984). Adults can exceed 120 mm total length and reach reproductive maturity in their fourth year (Lynch 1984). Females breed biennially (Lynch 1984) and although no Coeur d'Alene salamander nest has been observed in the wild, females presumably lay their eggs in a rock crevice and remain with their nests for several months as other Plethodons do (Nussbaum et al. 1983). Plethodontid salamanders are lungless, respiring through their skin and tissues lining the mouth (Spotila 1972).

Cutaneous respiration requires plethodontids to seek moist microhabitat, which occurs in moist soil or humid environments (Spotila 1972, Feder 1983, Grover 1998).

1.2 HABITAT ASSOCIATIONS

Across their geographic range, Coeur d'Alene salamanders require deep rock fissures to retreat from predators and harsh environmental conditions (Nussbaum et al. 1983). Potential Coeur d'Alene salamander habitat in the northern Rocky Mountains of Idaho occurs in areas with a minimum average precipitation of 50 cm and below 1,100 m elevation (Wilson & Larsen 1998). Coeur d'Alene salamanders are absent where unconsolidated materials occur (Wilson & Larsen 1998). In mountainous terrain, Coeur d'Alene salamanders need deep subterranean habitat to hibernate during the cold winters. During the spring, summer and fall, they likely retreat under cover objects and into rock crevices to hydrate and to avoid hot and dry conditions on a daily basis (Nussbaum et al. 1983, Cannings et al. 1999).

Coeur d'Alene salamanders occur in roadside seepages, waterfall splash zones, streamsides, talus mixed with soil, in caves, and in forest litter (Slater & Slipp 1940, Nussbaum et al. 1983, Lynch 1984, Wilson & Larsen 1988, Wilson 1993, Groves et al. 1996, Cannings et al. 1999). Occurrences in the southern portion of their range (Idaho and Montana) are associated with moderate to high canopy cover, high gradient slope, fractured bedrock, splash zones, seepages, high humidity, and talus mixed with soil on north facing slopes (Cassirer et al. 1994; Groves et al. 1996). Coeur d'Alene salamanders are nocturnal and their surface activity is limited by cold temperatures ($< 4^{\circ}\text{C}$) and hot ($> 15^{\circ}\text{C}$), dry (> 7 days since rain) weather (Wilson & Larsen 1988).

1.3 STATUS OF *PLETHODON IDAHOENSIS*

The Coeur d'Alene salamander is a species of Special Concern in Canada (COSEWIC 2007) and in the states of Montana (MNHP & MFWP 2006) and Idaho (IDFG 2005). It is the only species in the family Plethodontidae (lungless salamanders) that occurs in the northern Rocky Mountains of the United States (Nussbaum et al. 1983) and in the Columbia Mountains of British Columbia, Canada. Coeur d'Alene salamanders have specific habitat requirements and are considered the most closely associated with water of all western *Plethodon* species (Brodie 1970). They require moist retreats, as found within stream bank talus or fractured bedrock, to rehydrate following surface activities. Isolated and presumably small populations may be at risk of extirpation due to anthropogenic habitat disturbance (e.g., road construction and maintenance, diversion of water from streams, pollution, and forest harvesting) or catastrophic natural events (e.g., avalanches, debris flows).

Occupancy surveys of this elusive, nocturnal amphibian have recently expanded our knowledge of the species' range from the arid Southern Rocky Mountain Trench to the wet Columbia Mountains extending north of Revelstoke, BC (BC CDC 2007). Data on the abundance, age structure, and distribution within and among populations of Coeur d'Alene salamanders are deficient in Canada, yet this information is necessary to determine population trends and design conservation plans for preventing this salamander from becoming threatened or endangered.

Habitat selection and abundance can be measured at many spatial scales, from across the geographic range to selection of food items from those available. I studied Coeur d'Alene salamander habitat associations and relative abundance between and within sites

(750 m² - 1000 m²) on one mountain face (25 hectares). The objectives of my study were to (1) estimate the relative abundance, (2) describe the age structure, and (3) determine the microhabitat associations of Coeur d'Alene salamanders across an elevation gradient in Mt. Revelstoke National Park.

2 MATERIALS AND METHODS

2.1 STUDY AREA AND SITE SELECTION

In 2001, Coeur d'Alene salamanders were discovered among waterfalls, roadside seeps, and streams on the east bank of the Columbia River north of Revelstoke, B.C. (P. Ohanian, personal communication, February 15, 2006). Exploratory surveys in 2003 (Dykstra 2004) provided the first detection of Coeur d'Alene salamanders in Mount Revelstoke National Park (MRNP). The MRNP population is 95 km south of the most northerly occurrence (BC CDC 2007). Mount Revelstoke National Park is protected from resource extraction; however, the forest is mainly second growth following forest harvesting in the late 1870s for the construction of the Canadian Pacific Railway. The forested landscape is bisected by the Trans-Canada Highway in the Illecillewaet valley, Highway 23N along the Columbia River valley, and the Meadows in the Sky Parkway on Mt. Revelstoke.

Within the study area, the lower west-facing slopes of Mt. Revelstoke are dominated by the Thompson Moist Warm Interior Cedar-Hemlock Variant (ICHmw3) of the ICH biogeoclimatic zone (Braumandl & Curran 1992). At approximately 1000 m, colder temperatures are evident where the Wells Gray Wet Cool Interior Cedar-Hemlock Variant (ICHwk1) occurs. The climate at the Revelstoke airport, approximately 20 km from the study area, is characterized by 1278 mm average annual precipitation (Environment Canada 2004). January is the coldest month with a daily average minimum temperature of -8°C and the daily average maximum temperature, 25°C, occurs in July. The lower elevations are usually snow free by the end of May. The daily average temperature is above 6.5°C from April through October, which likely delineates the local salamander season of surface

activity in the valley bottom. Average monthly rainfall during this season varies between 52 mm in April to 79 mm in October.

The study area is located from 450 m to 1500 m on the southwest face of Mt. Revelstoke, B.C., in the Selkirk Range of the Columbia Mountains (Fig. 2.1). The coordinates of the entrance to Mt. Revelstoke National Park are 51°032.79''N, 118°126.46''W, which roughly corresponds with the southwest corner of the study area. Access and personal safety were the primary concerns when choosing streams for this study. Preliminary presence/no-detection surveys were conducted on watercourses originating from Mt. Revelstoke and flowing into the Illecillewaet and Columbia rivers east and north of the national park boundary to establish a list of candidate streams with salamanders present. There were several streams originating from Mt. Revelstoke and flowing into the Columbia River north of Revelstoke, these potential study streams were not selected due to dangerously steep gradients and inaccessible stream banks.

Presence/no-detection surveys of potential study sites began on May 9, 2006. The first salamanders of the season were detected on May 12, 2006 at two different waterfall sites. Salamanders were detected at 10 new locations and confirmed at 2 sites that were originally detected in 2001 (Appendix). Salamanders were not detected at 14 potential sites, including nine sites on Mt. Revelstoke, one site north of Revelstoke and four sites on streams east of Revelstoke (Appendix). To choose the study streams and begin the study as soon as possible, several potential sites were surveyed only once, which is an insufficient amount of survey effort to determine salamander presence or absence on these sites.

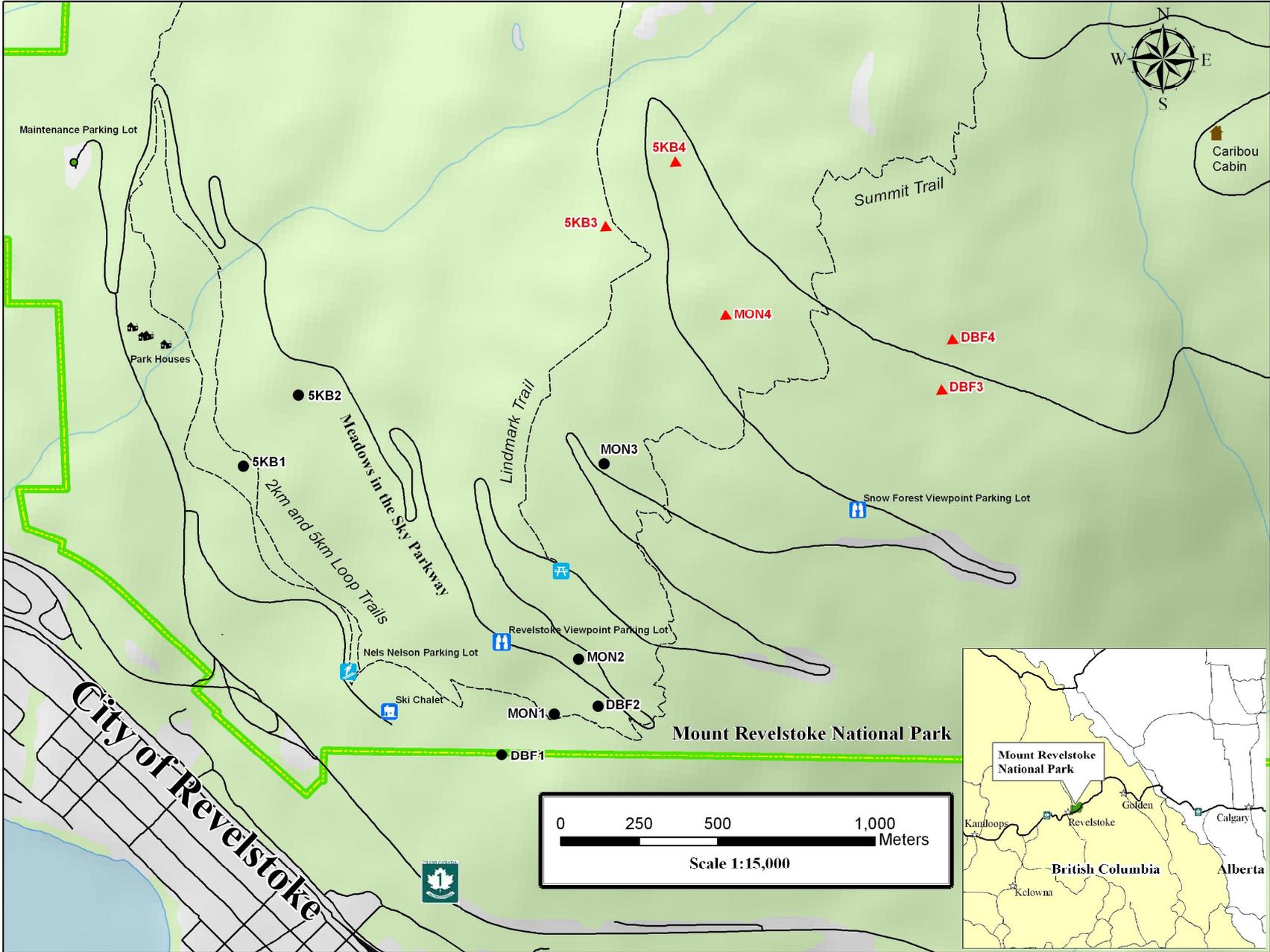


Figure 2.1: Map of the study area centered on Mount Revelstoke National Park of Canada. The area ranges from 450 m to 1400 m on the southwest facing slope of Mount Revelstoke, BC. Mount Revelstoke is located in the southeast corner of British Columbia (Inset). Study sites where salamanders were detected are indicated with black circles and study sites where no salamanders were detected over repeated surveys are indicated with red triangles. Map provided courtesy of Parks Canada.

By June 11, 2006, salamanders were detected on three streams, all flowing through the same forest type. These three previously nameless streams met the study selection criteria of: salamanders present, accessible, with acceptable risk for night travel, and with distinct channels that run from 1500 m to 450 m elevation. These streams were named 5KB (crosses the 5 km trail, Fig.2.2a), Monashee (MON), and Double Falls (DBF). I randomly generated an elevation between 500 m and 750 m to establish the start of the lowest study site on each of three streams. We hiked to these start locations and secured a 0 m marker with reflective tape. Another reflective marker was placed upstream to mark the end of each study site, establishing sites 5KB1, MON1, and DBF1. We hiked upstream for another 250 m and then marked the second transect per stream, 5KB2, MON2, and DBF2. The same procedure was followed to lay out two sites per stream above 950 m elevation (MON3, MON4, 5KB3, 5KB4, DBF3, and DBF4). This design resulted in four sites per stream, including two in each elevation band, for a total of 12 study sites (Fig. 2.1).

2.2 SALAMANDER SURVEYS

Three visual encounter surveys of each low elevation site (6 sites) were conducted in June and three surveys of all 12 sites were conducted in August in an attempt to collect enough capture-mark-recapture data to estimate the population size. In addition, three surveys of one site (MON2) were repeated in July and September to provide monthly data for detecting changes in relative abundance throughout the season of surface activity. In June, the upper elevation sites were still snow covered; therefore, salamanders were not expected to be active on the surface. In August, we were able to survey all 12 study sites in random order, three times each. We surveyed an average of two sites per night, selecting sites in random order.

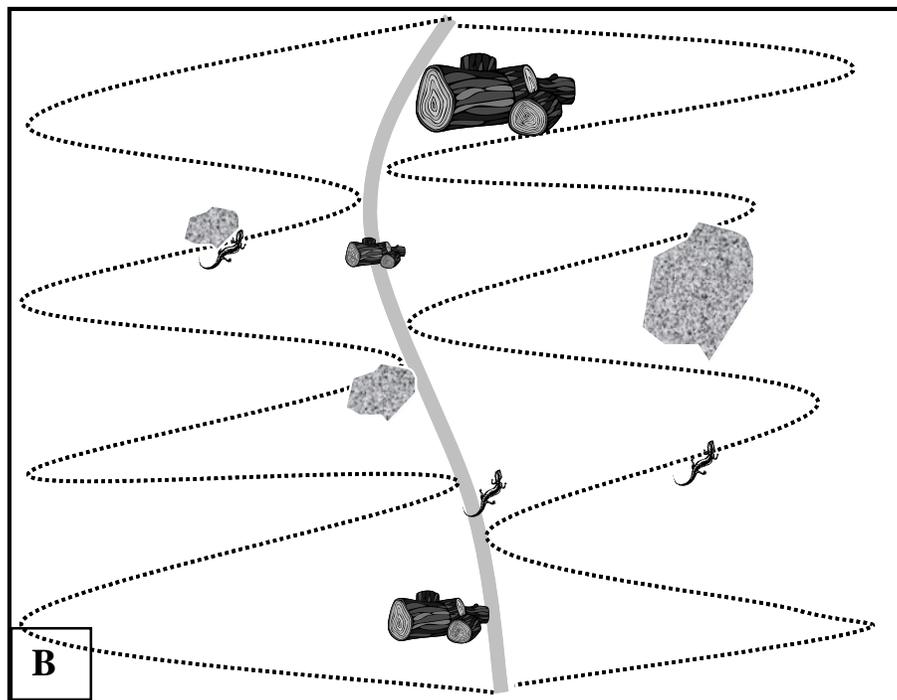
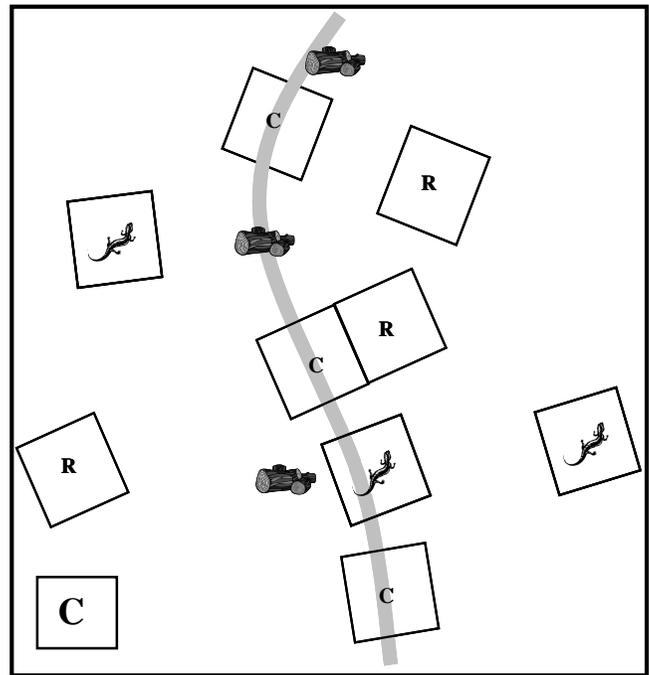


Figure 2.2: (A) Study stream 5KB in Mount Revelstoke National Park, (Black and White photo). (B) Walk-and-turn survey method used during nocturnal visual encounter surveys for Coeur d’Alene salamanders. Sites were 10 m wide centered on the stream and 75-100 m along the stream. (C) Habitat characteristics were measured at salamander capture locations and every 5 m along stream at stream centre (C) and random (R) distances (1-5 m) on either side of the stream.

The surveys commenced at least one hour after sunset. Survey teams of two to three people used a walk-and-turn method to survey all of the area within the site. For example, a team of two would begin at stream centre at the bottom of the site and walk in opposite directions out to the 5 m boundary, always angled upstream from the start point. At the 5 m boundary, the observer would turn and walk back to stream centre, always proceeding at an upstream angle (Fig. 2.2b). The observers used headlamps to continuously search the ground surface, only stopping to gently turn objects that could be easily lifted and replaced without significant disturbance to the forest floor in search of salamanders. We searched the forest floor, on and under downed wood, under bark, among exposed rock, tree trunks, and stumps for salamanders. Depending on the salamander species, natural cover searches yield higher counts and lower spatial and temporal variation across surveys than those using artificial cover boards (Hyde & Simons 2001).

Salamanders were captured by hand as they were encountered and each individual was placed in a resealable bag (16.5 cm x 8.2 cm) with a small amount of stream water, wet leaves or moss, and an air pocket. Salamanders were captured and held for 4 hours before they were weighed, measured, individually marked, and released at their capture locations. Each salamander was weighed in the bag to the nearest 0.1 g with a Pesola© 10 g spring scale and then each bag was weighed separately after the salamander was released. The mass of the salamander was determined by subtracting the bag mass from the total salamander + bag mass. While still encased in the bag, a ruler was laid along the length of each salamander and total length and snout-vent-length (SVL) were recorded to the nearest mm. SVL was recorded from the tip of the snout to the front of the vent (Corkran & Thoms 1996). Salamanders were classified into one of three life stages based on SVL: neonate, juvenile, or adult. It is difficult to positively identify the sex and life stage of Coeur d'Alene salamanders

in the field; therefore sex information was not recorded and life stages were arbitrarily set following the work of Lynch (1984).

Salamanders greater than 18 mm SVL were uniquely marked with an injection of a fluorescent, biocompatible, silicone-based material (elastomer) beneath the skin along one or several salamander limbs (ventral surface). The non-toxic elastomer was injected as a liquid with a 0.3 ml injection syringe. The elastomer quickly cures into a pliable solid that remains externally visible. These Visible Implant Elastomer (VIE) tags are widely used for marking “finfish, crustaceans, reptiles, and amphibians” (NMT 2006). The syringe needle was disinfected with an alcohol wipe between injections of individual salamanders. All equipment and footwear were disinfected between sites with a solution of 1 part chlorine bleach to 10 parts water.

Environmental conditions were recorded for each site immediately prior to each salamander survey at a streamside location. These included weather (rain, clear, cloudy), ambient air temperature and relative humidity 1 m from the ground as well as substrate (litter, moss, soil) temperature, water temperature, and relative ground moisture (dry, moist, wet, saturated). Ambient air temperature was recorded again at the end of each salamander survey. At each salamander capture location, substrate type, substrate temperature, distance to water, elevation, ambient temperature, and relative humidity were recorded. Within the survey area, braided stream channels and pools of surface water were included in distance to water measurements. Following release of each salamander, the substrate to which the individual retreated was recorded. Each capture location was marked on the site with a wire-stemmed flag on which the salamander’s tag identity was recorded.

2.3 HABITAT DATA

Available habitat was systematically sampled in 1-m² quadrats placed every 5 m along the centre of the stream channel and at a random horizontal distance (1-5 m) on either side of stream centre (Fig. 2.2c). Within each quadrat, elevation, gradient, and aspect were recorded (Table 2.1). The vegetation community was characterized by percent cover and species of trees, shrubs, forbs, and grasses. Substrate was characterized by percent cover of bryophyte, litter, bedrock, boulders, cobbles, gravel, sand, soil, tree stems, and downed wood. The percent of each quadrat covered by standing water or where the stream was braided and flowing in many rivulets was also recorded. The same variables were recorded for each of the 1-m² habitat quadrats centered on the wire flag for each salamander capture location, representing *used* microhabitat.

In the habitat analysis, the heterogeneous physical features of the stream reaches surveyed were divided into two more homogenous categories. These included the Stream Habitat Area (= average bank width (m) x site length (m)) and the Terrestrial Habitat Area (= Total Site Area (m²) - Stream Habitat Area (m²)). The stream habitat is defined as having been altered by water flow, while the terrestrial area as not. In the statistical analysis, this was addressed by separating plots that fell within the bank width of the stream (STREAM plots) and those that did not (TERRESTRIAL plots). The STREAM data set included all randomly selected streambed plots plus a portion of the stream centre plots (sampled every 5 m) ensuring that available stream habitat was sampled relative to the total proportion of stream habitat available.

Table 2.1: Continuous variables were used in exploratory factor analysis of stream and terrestrial habitat up to 5 m beyond stream centre on seven study sites in Mount Revelstoke National Park, Canada. Data were collected on seven sites on three streams where Coeur d’Alene salamanders were detected during the summer of 2006. Continuous (Con) and categorical (Cat) variables were considered for logistic regression (LR) analysis. LR was applied to investigate the relationship between the habitat characteristics of used and available 1-m² quadrats along streams inhabited by Coeur d’Alene salamanders.

	Variable	Abbreviation	Data	Units	Description
Stream Channel Morphology ¹	Stream Centre Gradient	S_gra	Con	°	Gradient of streambed measured with a clinometer at stream centre
	Bank Width	BW	Con	cm	Width of the stream channel from high water mark to high water mark on each bank
	Left Bank Gradient	LB_gra	Con	°	Gradient of the left stream bank facing upstream, measured with a clinometer
	Right Bank Gradient	RB_gra	Con	°	Gradient of the right stream bank facing upstream, measured with a clinometer
	Left Bank Aspect	LB_asp	Con	°	Aspect (degrees) measured with a compass at the stream bank facing stream centre
	Right Bank Aspect	RB_asp	Con	°	Aspect (degrees) measured with a compass at the stream bank facing stream centre
	Left Bank Substrate	LB_sub	Cat		The dominant substrate on the stream bank (bedrock, boulder, cobble, gravel, sand, soil, downed wood, tree, moss, litter)
	Right Bank Substrate	RB_sub	Cat		The dominant substrate on the stream bank (bedrock, boulder, cobble, gravel, sand, soil, downed wood, tree, moss, litter)
	Left Bank Cover	LB_cov	Cat		The dominant cover on the stream bank (tree, shrub, downed wood)
	Right Bank Cover	RB_cov	Cat		The dominant cover on the stream bank (tree, shrub, downed wood)
	Habitat Type	Htype	Cat		The dominant stream descriptor: Run, Step_pool, Braided, Underground
	Water Volume	W_vol	Cat		Subjective observations: High, Moderate, Low, Very Low

¹ Stream channel variables were recorded every 5 m along the stream

	Variable	Abbreviation	Data	Units	Description
Quadrat Scale	Elevation	Elev	Con	m	Height (meters) above sea level measured with an altimeter
	Quadrat Aspect	Q_asp	Con	°	Aspect (degrees) measured with a compass at the centre of each quadrat
	Quadrat Gradient	Q_gra	Con	°	Gradient measured with a clinometer at the centre of each quadrat
	Water Cover	Wcov	Con	%	Visual estimate of the percent of water covering substrate within each 1-m ² quadrat
	Stream Distance	S_dis	Con	cm	Distance in cm from the centre of the quadrat to the edge of the stream flow
	Canopy Cover	Ccov	Con	%	Visual estimate of the percent of canopy coverage directly above each 1-m ² quadrat
Vegetative Cover	Bryophyte Cover	Bcov	Con	%	Visual estimate of the percent of moss covering any substrate within each 1-m ² quadrat
	Grass Cover	Gcov	Con	%	Visual estimate of the percent of grass covering each 1-m ² quadrat
	Shrub and Forb Cover	Shcov	Con	%	Visual estimate of the percent of shrub and forb covering each 1-m ² quadrat
	Litter Cover	Lcov	Con	%	Visual estimate of the percent cover of litter on the ground surface within each 1-m ² quadrat
	Tree	TREE	Con	%	Visual estimate of the percent cover of tree stems within each 1-m ² quadrat
Substrate Proportion	Bedrock	bed	Con	%	Visual estimate of the percent cover of bedrock exposed within each 1-m ² quadrat
	Boulder	Boul	Con	%	Visual estimate of the percent cover of boulders (> 250 mm) within each 1-m ² quadrat
	Cobble	Cobb	Con	%	Visual estimate of the percent cover of cobbles (65 - 249 mm) within each 1-m ² quadrat
	Gravel	Grav	Con	%	Visual estimate of the percent cover of gravel (2 - 64 mm) within each 1-m ² quadrat
	Sand	Sand	Con	%	Visual estimate of the percent cover of sand within each 1-m ² quadrat
	Soil	Soil	Con	%	Visual estimate of the percent cover of bare ground within each 1-m ² quadrat
	Downed Wood	DW	Con	%	Visual estimate of the percent cover of downed wood on the ground within each 1-m ² quadrat

2.4 STATISTICAL ANALYSES

Many sources of variation may explain the abundance and distribution of salamanders along watercourses. Here the variation in salamander relative abundance was explored according to elevation (low, high), stream (5KB, DBF, and MON), and life stage (adult and juveniles plus neonates). Neonates were pooled with juveniles as there were too few neonates to analyze separately. Although time (of survey) may also explain some variation in the number of salamanders captured, there was too much temporal variability among surveys within sites to model the effect. Therefore, in the abundance analyses, averages were calculated on total salamanders caught over three surveys of each site.

The relative amount of variation in salamander abundance between the two elevation bands and among the three streams was determined by averaging the sum of salamanders caught over three surveys in August 2006 on each of 12 sites. The count data were not normally distributed and attempts to transform the count variable to approximate a normal distribution were not successful. Therefore, I conducted a two-way analysis of variance with stream and elevation band as the two main factors. Salamander relative abundance was modeled using PROC GENMOD in SAS (SAS v.9.1.3, SAS Inc., Cary, NC) specifying the Poisson distribution, and using survey area as an offset to standardize across sites. Estimates of variation are given as ± 1 standard error of the mean in all statistical statements below. Variation in salamander relative abundance between factors was considered significant if $p < 0.05$. The standard Bonferonni correction for multiple comparisons was applied for between-group comparisons to preserve an overall probability level of $\alpha = 0.05$.

A more detailed summary of the life stage distribution in the study area was provided by including data from three surveys in June 2006, soon after the salamanders emerged from

hibernation, in addition to the data from three August 2006 surveys. All six surveys were conducted on the stream sites below 950 m. With this broader data set, the size class distribution between the June surveys and the August surveys was compared.

To estimate the population size, a table reporting the capture history for salamanders caught and recaptured during three surveys in each month (June and August), was constructed as recommended by Krebs (2001). However, the recapture rate ($\text{Total Marked} / \text{Total Captured} = 10/253 = 3.95\%$) was too low to calculate a meaningful population estimate. Therefore, the number of salamanders captured per 1000 m² on each site was calculated as the measure of relative abundance among six sites in June, among 12 sites in August, and for MON2 in June, July, August, and September.

2.4.1 Habitat description

Factor analysis was used to describe the habitat among the 12 study sites by reducing the number of variables into factors that summarize the correlations among the explanatory variables. Stream and terrestrial habitat were analyzed separately. Available quadrats were included in this analysis and quadrats used by salamanders were excluded. There were 256 observations in the STREAM data set and 380 observations in the TERRESTRIAL data set. The CPUE used to illustrate each site's factor scores was based on the average number of salamanders caught per survey of each site, standardized by site area.

Only continuous variables were included in the site-level habitat analysis (Table 2.2). Several variables had a large proportion of zeros and data were collected at the microhabitat scale (1-m²), therefore variables were summarized as means for each site (N = 12) by habitat type = Stream or Terrestrial and analyzed with PROC Factor (SAS v.9.1.3, SAS Inc., Cary, NC). A variable was only retained in the data-set if the variable had some correlation with at

least one other variable. Twenty-one variables were included in the analysis, capturing several categories of habitat features that may influence salamander occurrence (Table 2.2).

Table 2.2: Continuous variables (mean \pm 1 SE) used in the site level habitat description factor analysis, stratified by habitat type (streambed and terrestrial).

Variable	Streambed	Terrestrial
Stream centre gradient	18.5 \pm 12.1	17.3 \pm 11.9
Bankfull width	227.5 \pm 248.4	145.0 \pm 100.5
Left bank gradient	38.9 \pm 24.5	40.6 \pm 25.1
Right bank gradient	37.9 \pm 23.7	38.3 \pm 24.2
Quadrat aspect	134.3 \pm 37.0	121.0 \pm 41.9
Quadrat gradient	19.3 \pm 12.7	22.3 \pm 12.6
Water cover	29.9 \pm 33.9	0.9 \pm 6.1
Elevation	888.1 \pm 242.2	928.6 \pm 254.4
Canopy cover	64.9 \pm 37.9	76.0 \pm 33.1
Bryophyte cover	23.0 \pm 24.4	17.4 \pm 23.4
Grass cover	1.3 \pm 5.8	1.5 \pm 7.3
Shrub cover	17.7 \pm 24.4	37.1 \pm 34.0
Litter cover	24.4 \pm 30.7	67.9 \pm 33.4
Bedrock	1.8 \pm 8.9	0.1 \pm 1.4
Boulder	8.8 \pm 16.4	2.0 \pm 8.6
Cobble	18.0 \pm 26.7	2.2 \pm 10.2
Gravel	8.4 \pm 16.7	0.6 \pm 5.5
Sand	3.5 \pm 10.7	0.5 \pm 4.1
Soil	5.8 \pm 17.7	2.3 \pm 11.9
Downed wood	10.9 \pm 17.0	9.1 \pm 16.4
Tree	0.3 \pm 2.3	2.1 \pm 8.8

2.4.2 Microhabitat associations

Logistic regression is used by ecologists to model wildlife habitat use versus availability (Manly et al. 2002; Keating & Cherry 2004; Johnson et al. 2006). I applied logistic regression to model Coeur d'Alene salamander microhabitat. The dichotomous variable was USE (1 = Used, 0 = Available) and stream and terrestrial plots were analyzed separately. Three used plots that overlapped with three random available plots were eliminated to avoid contaminating the available habitat sample (Thomas & Taylor 2006).

Variable selection for the logistic regression analysis was achieved over several steps. Three variables were eliminated due to a high percentage of missing values, which would act to remove the entire observations if included in the model. Non-parametric two-sample t -tests were conducted on each continuous variable to determine if there was a statistically significant difference between the USED = 1 and the USED = 0. The univariate t -test results were compared with univariable logistic regression results. Variables with a $P < 0.25$ in both univariate analyses were included in the preliminary stepwise logistic regression procedure (Hosmer & Lemeshow 2000), conducted in SAS (SAS v.9.1.3, SAS Inc., Cary, NC). Several *a priori* models were specified based on a review of habitat associations from unpublished and published works, the results of the site-level analysis in this study, and subsets of the global model parameters. The model with the lowest Akaike's information criterion corrected for small sample size (AIC_c) was considered the most parsimonious model for each habitat type.

3 RESULTS

3.1 SALAMANDER RELATIVE ABUNDANCE

Coeur d’Alene salamanders were detected at seven of 12 sites, where each was surveyed a minimum of four times (Fig. 3.1). The highest elevation at which salamanders were detected was 980 m (on site MON3). In June 2006, 73 Coeur d’Alene salamanders were captured over three surveys at the six sites below 950 m. In August 2006, 180 Coeur d’Alene salamanders were captured over three surveys at the same six sites. Three salamanders were captured on MON3 in August, bringing the August total captures to 183. The average abundance of salamanders increased from June to August on five of six sites (Fig. 3.2). The abundance of salamanders on MON2 was slightly lower in August than in June (Fig. 3.2).

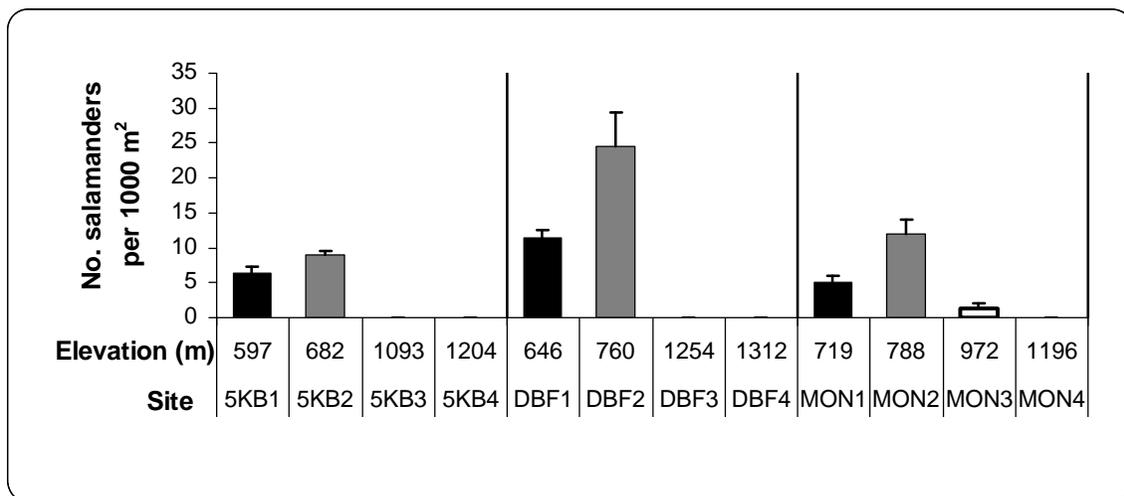


Figure 3.1: Mean abundance of Coeur d’Alene salamanders (± 1 SE) estimated from three nocturnal visual encounter surveys of each site in Mount Revelstoke National Park during August 2006. Three surveys were conducted on four sites (1-4) on each of three streams (abbreviated 5KB, DBF, and MON).

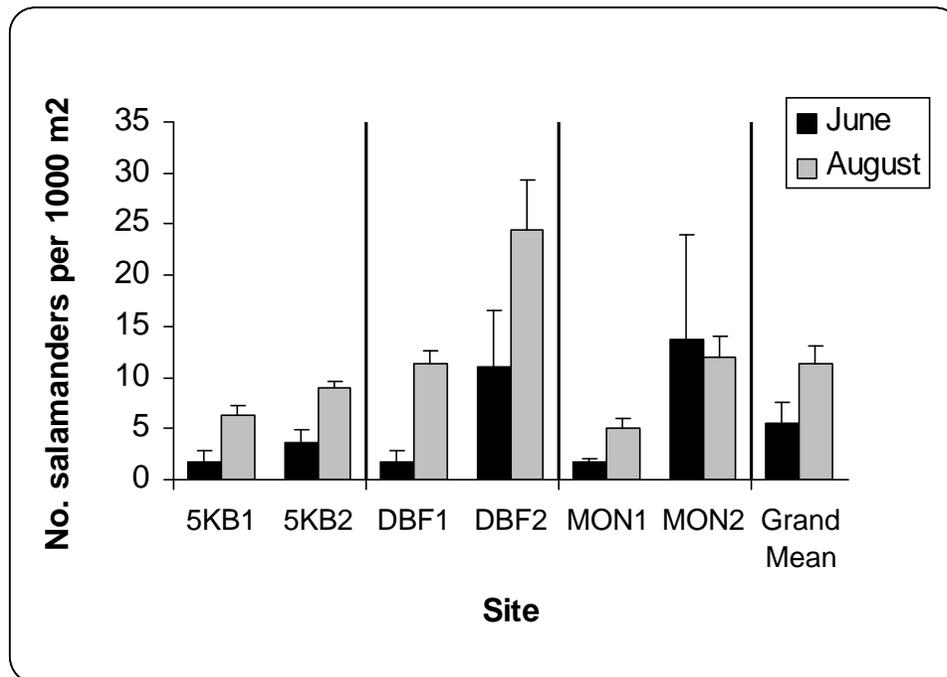


Figure 3.2: Mean abundance of Coeur d'Alene salamanders (± 1 SE) estimated from three nocturnal visual encounter surveys of six study sites accessible both in June and in August 2006. Visual encounter surveys were conducted after dark on two sites per stream (abbreviated 5KB, DBF, and MON) in Mount Revelstoke National Park.

No salamanders were detected above 1000 m during the repeated surveys of all 12 sites in August 2006. The lowest abundance of salamanders (1.3 ± 0.77 salamanders per 1000 m^2) was found on MON3 at 972 m (Fig. 3.1). Salamanders were most abundant (24.45 ± 4.95 per 1000 m^2) at 760 m on DBF2 (Fig. 3.1). No recaptures were recorded during the second and third surveys in June. Two bouts (June and August) of three surveys of each lower elevation site yielded 10 recaptured individuals from a total of 253 salamanders, resulting in a 3.95 % recapture rate.

In my analysis of salamander abundance, the main sources of variation were Stream and Elevation. The interaction between Stream (5KB, DBF, MON) and Elevation (low, high) was not significant so it was dropped from the final model. Elevation (low, high) was a statistically significant variable explaining the difference in salamander abundance along

watercourses on Mt. Revelstoke ($F_{1,8} = 43.58$, $P = 0.0002$, Fig. 3.3). The variation between streams was not statistically significant ($F_{2,8} = 2.81$, $P = 0.1192$, Fig. 3.3).

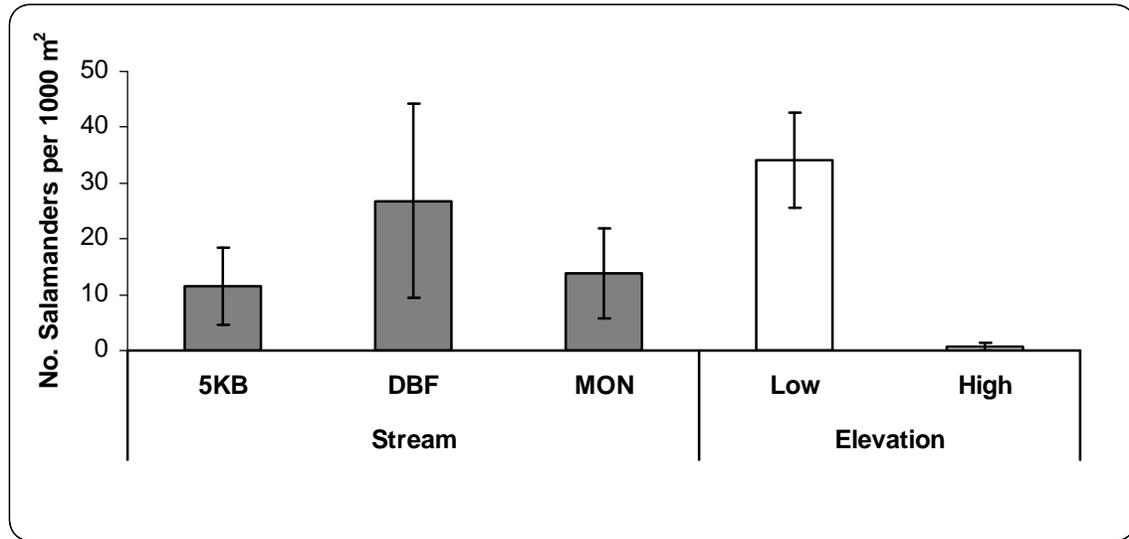


Figure 3.3: Mean abundance of Coeur d'Alene salamanders (± 1 SE) averaged across four sites per stream (abbreviated 5KB, DBF, and MON) during August 2006 on Mount Revelstoke, BC. Relative abundance was estimated from the sum of salamanders captured during three visual encounter surveys of each site standardized by area searched. In each elevation stratum (Low < 950 m < High), mean salamander abundance was estimated across six sites, two sites per stream (5KB, DBF, and MON).

3.2 AGE STRUCTURE

In this study, snout-vent-length (SVL) was analyzed as an approximation of the age class distribution throughout the salamander population (Fig. 3.4). In June, the proportion of juveniles (including neonates) across the three study streams ranged from 0.23 on DBF to 0.33 on MON (Fig. 3.5). The proportions of adults and juveniles among streams were similar in June (Fig. 3.5), but varied more in August (Fig. 3.6). The proportion of neonates decreased from June (0.13) to August (0.02) across the six lower elevation sites (Table 3.1). The juvenile size class made up a similar proportion of total salamander captures in both June (0.20) and August (0.17) (Table 3.1). Over the summer the proportion of adults increased from 0.67 in June to 0.81 in August. The monthly data for MON2 suggested the

neonate proportion decreased from June to July and then remained low (0.02 – 0.05). The proportion of juveniles on MON2 fluctuated among months and the adult proportion was relatively consistent (0.45 – 0.52). The adult proportion of the salamanders captured on MON2 in August (0.81) mirrors the proportion of adult salamanders across the six sites in that month (0.81).

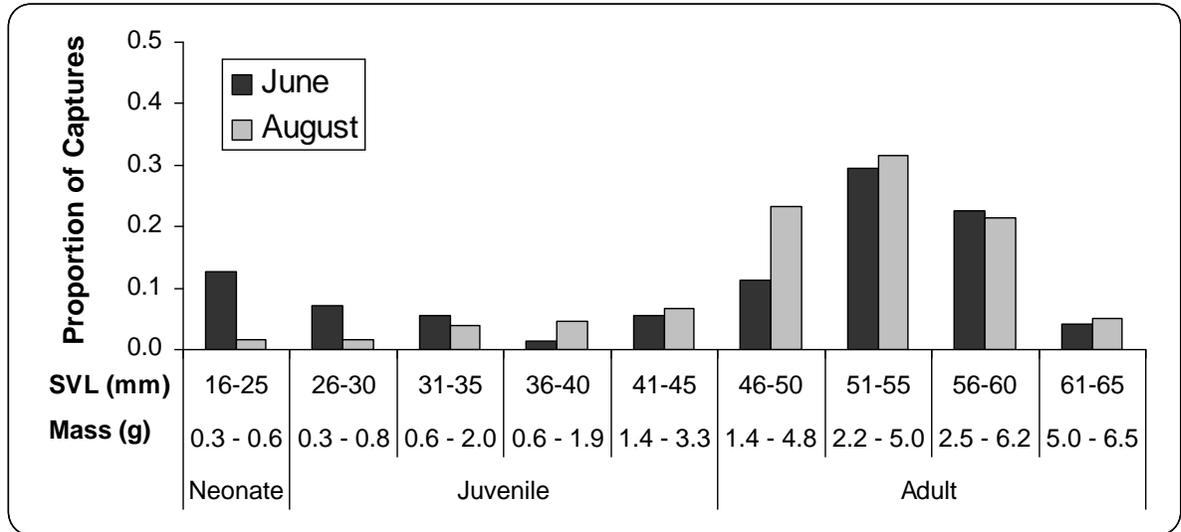


Figure 3.4: Size-class distribution of Coeur d'Alene salamanders on Mount Revelstoke, BC in June and August 2006. Visual encounter survey observations were summed across three surveys of six sites, two sites on each of three streams, in June and repeated in August 2006. Life stages followed Lynch (1984).

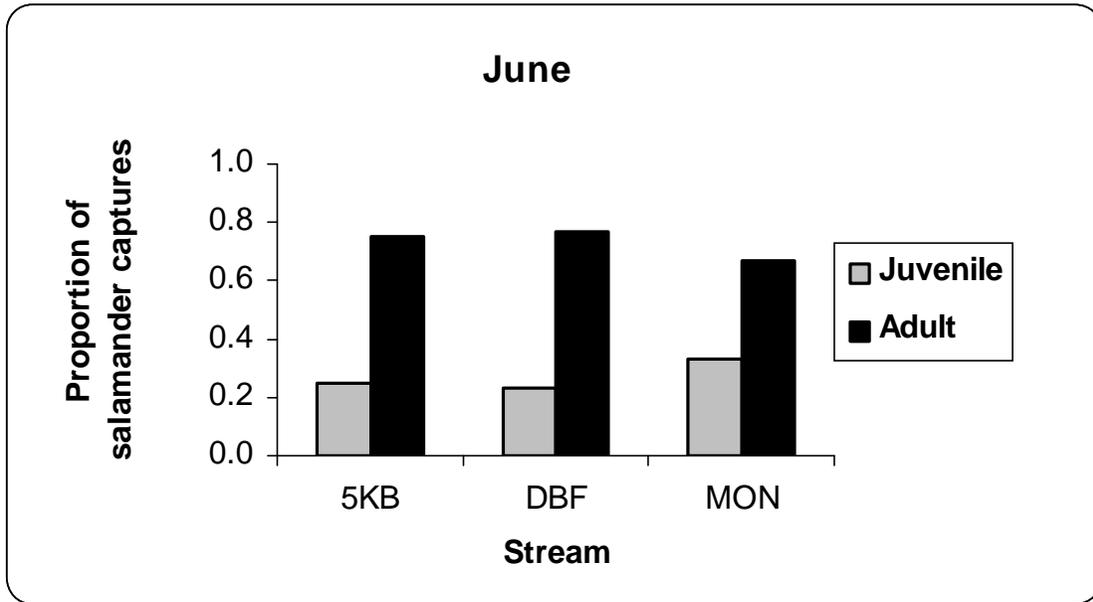


Figure 3.5: The proportions of juvenile and adult Coeur d'Alene salamanders on three streams on Mount Revelstoke, BC in June 2006. Proportions are based on total salamanders captured over three visual encounter surveys of two sites (below 950 m) per stream (abbreviated 5KB, DBF, and MON) in June 2006.

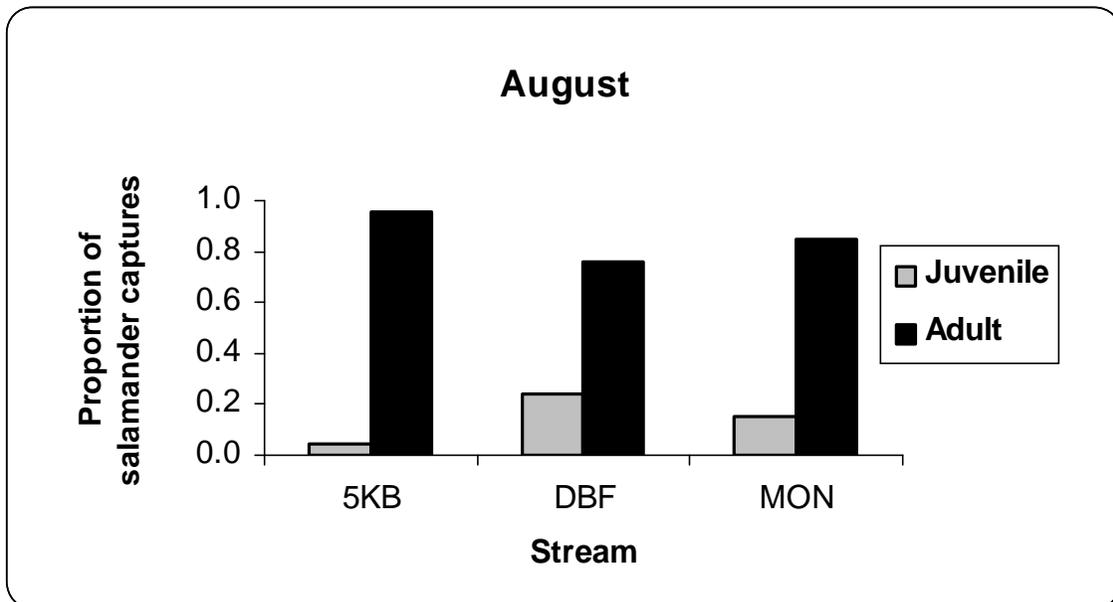


Figure 3.6: The proportions of juvenile and adult Coeur d'Alene salamanders on three streams on Mount Revelstoke, BC in August 2006. Proportions are based on total salamanders captured over three visual encounter surveys of two sites (below 950 m) per stream (abbreviated 5KB, DBF, and MON) in August 2006.

Table 3.1: Monthly variation in Coeur d’Alene salamander life stage proportions from June to September 2006 on site MON2. Life stages were based on snout-vent-length categories following Lynch (1984). Salamander captures on MON2 were summed across three surveys per month. The mean salamanders of six sites was estimated from three surveys of two sites on each of three streams (abbreviated MON, 5KB, and DBF) in June and repeated in August of 2006 on Mount Revelstoke, B.C.

	June		July	August		September
	MON2	Mean of 6 Sites	MON2	MON2	Mean of 6 Sites	MON2
Neonates	0.24	0.13	0.05	0	0.02	0.04
Juveniles	0.24	0.20	0.50	0.19	0.17	0.46
Adults	0.52	0.67	0.45	0.81	0.81	0.50

Coeur d’Alene salamander abundance on MON2 was lowest in July and moderate in June and August (Fig. 3.7). The abundance of salamanders increased dramatically in September, mostly accounted for by an increase in the abundance of juvenile salamanders (Fig. 3.7).

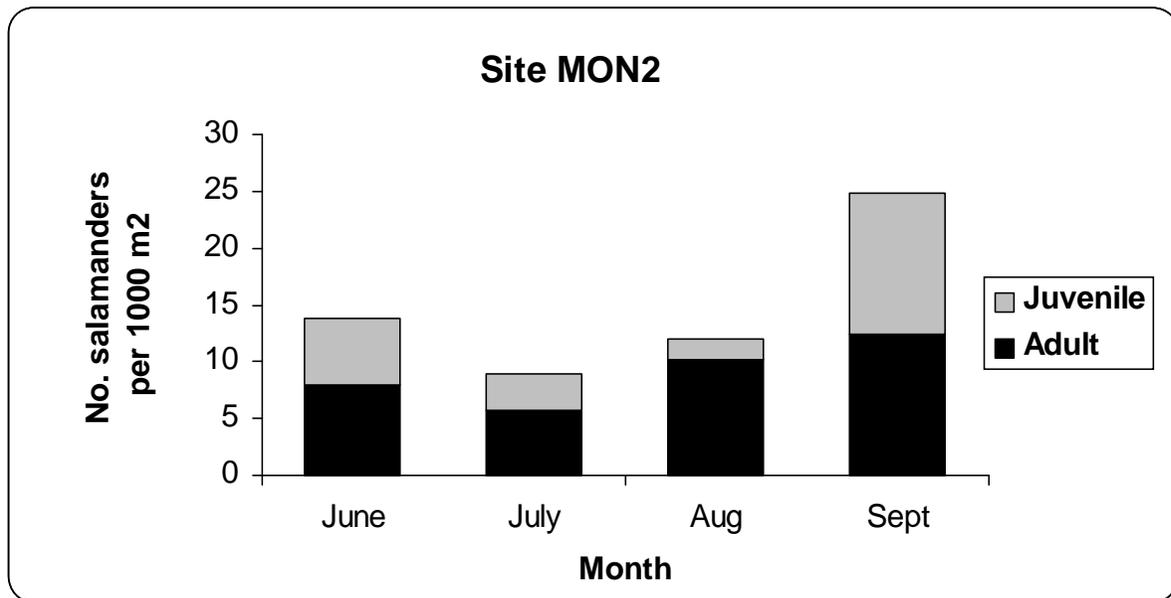


Figure 3.7: Mean abundance of juvenile and adult Coeur d’Alene salamanders estimated from three nocturnal visual encounter surveys per month (June – September 2006) of site MON2 in Mount Revelstoke National Park, Canada.

3.3 DISTRIBUTION

I examined the distribution of Coeur d'Alene salamanders captured in the streambed and in the terrestrial habitat up to 5 m beyond the stream centre. The maximum distance between salamander locations was 25 m within 75 m to 100 m long sites. Fifty-eight percent of salamanders were captured within 50 cm of water (Fig. 3.8). Salamanders were observed up to 10 m away from water beyond the boundaries of the study sites.

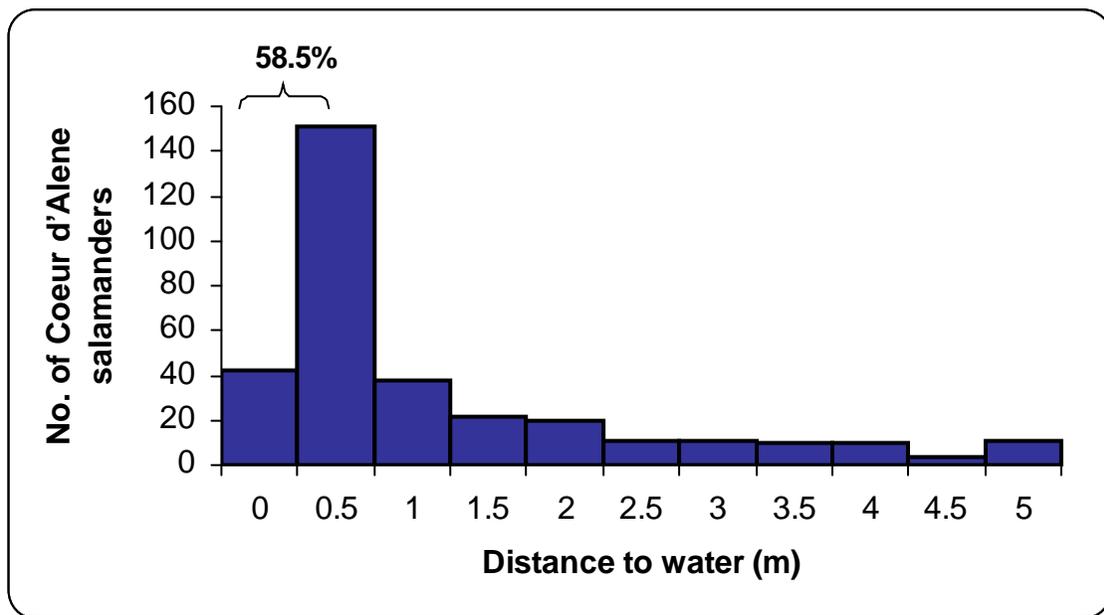


Figure 3.8: Distribution of Coeur d'Alene salamander captures by distance to surface water during nocturnal visual encounter surveys from June through September 2006 on Mount Revelstoke, BC. Distance from the salamander capture location to the nearest standing water pool or stream flow was recorded at the time of capture.

Average proportions were calculated separately for salamanders captured in stream versus terrestrial habitat across the six lower elevation sites (500 m to 950 m elevation). The proportion of stream habitat available was 0.22; the remaining 0.78 of the total area was classified as terrestrial habitat (Available Habitat; Fig. 3.9). Salamanders were detected in

the streambed proportionately more often (0.39 – 0.79) relative to the area of stream habitat available during five of six salamander surveys (Fig. 3.9).

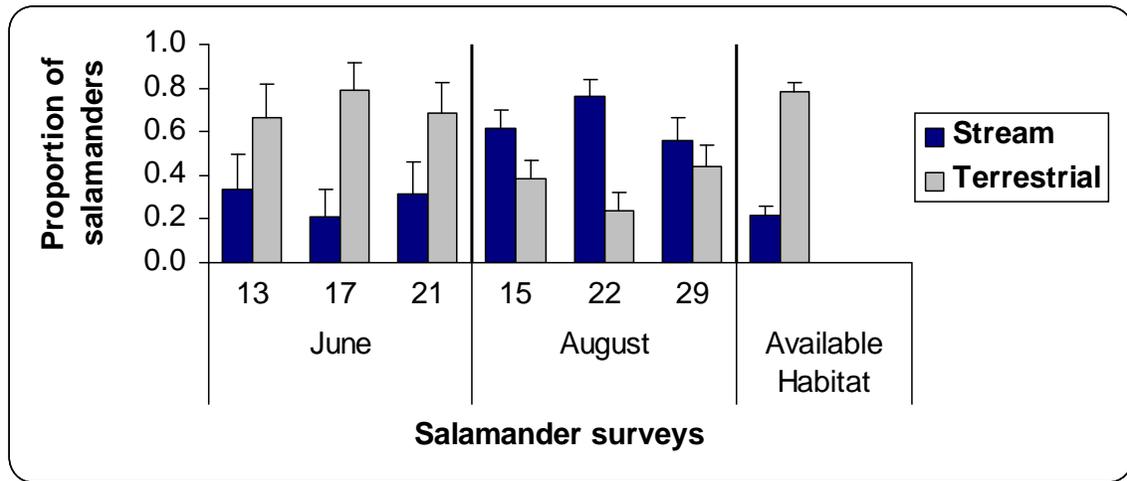


Figure 3.9: Mean proportion of Coeur d’Alene salamanders (+ 1 SE) captured in stream and terrestrial habitat during three surveys in June 2006 and August 2006 on Mount Revelstoke. Mean proportion was estimated across six sites below 950 m, two sites on each of three streams. The average proportion of stream and terrestrial habitat available across the six sites surveyed is displayed in the far right column.

In June, the proportion of stream to terrestrial habitat used by adult salamanders was similar to the proportions of available habitat (Fig. 3.10). In August, adult and juvenile salamanders used stream habitat proportionately more than the stream habitat available (Fig. 3.10). Juvenile salamanders were detected in stream habitat proportionately more than the stream habitat available in June and August (Fig. 3.10).

A drop in ambient air temperature during the June 17 surveys coincided with a decrease in the proportion of salamanders found in streambeds (Fig. 3.11). As average temperature increased during the June and August surveys, so did the proportion of salamanders found in stream habitat. In August, the ambient temperature remained above 15°C, a period during which salamanders were found proportionately more in the streambed (Figs. 3.9, 3.10, 3.11).

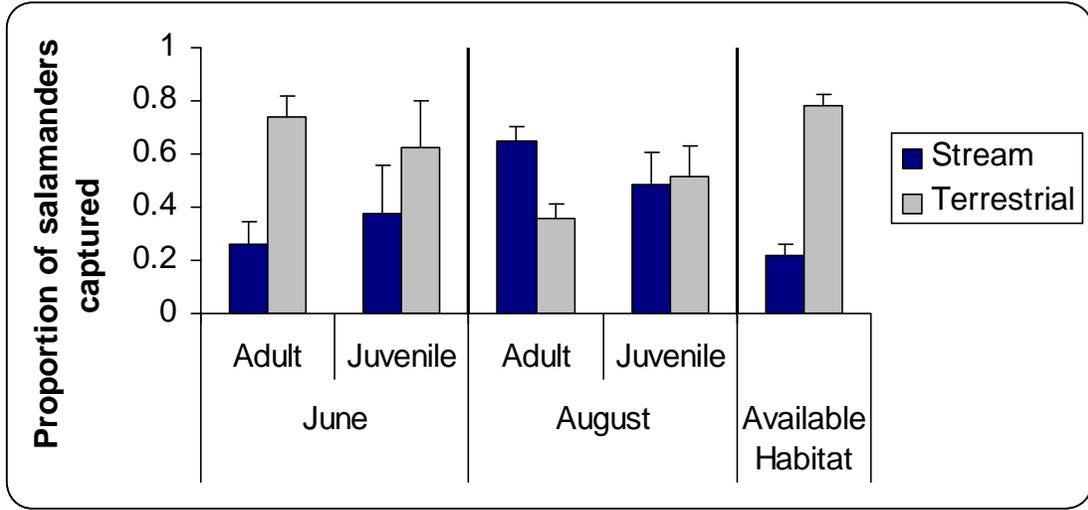


Figure 3.10: Mean proportion of adult and juvenile Coeur d’Alene salamanders (+ 1 SE) captured in stream and terrestrial habitat on Mount Revelstoke in June and August 2006. Mean proportion of stream and terrestrial habitat used by each life stage in June and August 2006 was estimated across six sites below 950 m, two sites on each of three streams. The average proportion of stream and terrestrial habitat available across the six sites surveyed is displayed in the far right column.

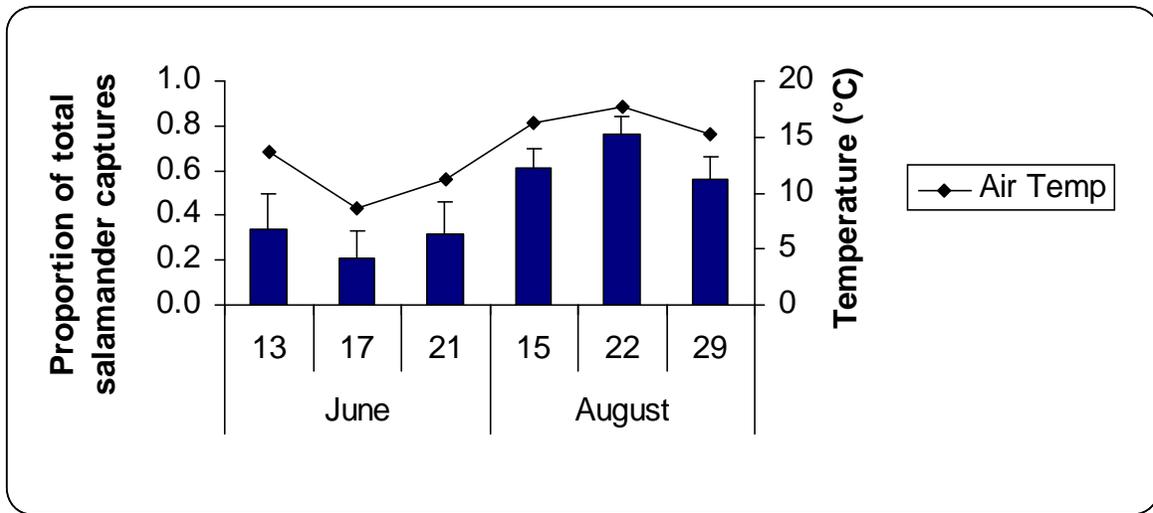


Figure 3.11: Mean proportion (+ 1 SE) of Coeur d’Alene salamanders within stream habitat on Mount Revelstoke, BC in June and August 2006 relative to the average air temperature during the surveys. Mean proportion was estimated across six sites below 950 m, two sites per stream. The average air temperature was estimated from measurements taken at the beginning of each visual encounter survey. Visual encounter surveys were conducted on six sites in June and August 2006 and repeated three times per month.

3.4 HABITAT DESCRIPTION

3.4.1 Stream habitat

I used factor analysis to reduce and summarize stream habitat data into a small number of factors that accounted for correlations among the original variables. The original 21 continuous variables were reduced to eight variables and two or three explanatory factors that have biological meaning. Factor 1 isolated stream gradient, quadrat gradient, and boulder cover (Table 3.2). Stream and quadrat gradient combined with boulders in the streambed describe the geomorphologic features of the streams. Factor 2 isolated water cover and bedrock, with a negative correlation to elevation, suggesting that more surface water in the lower elevation stream reaches was associated with exposed bedrock. Factor 3 isolated the stream bank gradient, suggesting channel shape on a continuum from V to flat is a valid descriptor of the study sites. The two factor and three factor models isolated the same variables on Factor 1 (geomorphology) and Factor 2 (surface water), while Factor 3 (bank gradient) was dropped from the two factor model (Tables 3.2, 3.3).

Table 3.2: Three factor model resulting from exploratory factor analysis of stream habitat variables that describe Coeur d’Alene salamander habitat along streams on Mount Revelstoke, BC. Values represent the correlations between variables and the explanatory factor, also called factor loadings. Bold values indicate the variables that load primarily on a single Factor, from which the factor descriptor (in parentheses) is derived.

Variable	Factor 1 (Geomorphology)	Factor 2 (Surface water)	Factor 3 (Bank gradient)
Stream gradient	0.974	-0.128	0.107
Quadrat gradient	0.993	-0.026	0.047
Boulder	0.827	0.209	0.222
Water cover	-0.081	0.884	0.062
Elevation	-0.029	-0.923	0.032
Bedrock	0.079	0.825	0.053
Left bank gradient	0.292	-0.053	0.912
Right bank gradient	0.021	0.002	0.933

Table 3.3: Two factor model resulting from exploratory factor analysis of stream habitat variables that describe Coeur d'Alene salamander habitat along streams on Mount Revelstoke, BC. Values represent the correlations between variables and the explanatory factor, also called factor loadings. Bold values indicate the variables that load primarily on a single factor, from which the factor descriptor (in parentheses) is derived.

	Factor 1 (Geomorphology)	Factor 2 (Surface water)
Quadrat gradient	0.989	-0.032
Stream gradient	0.978	-0.129
Boulder	0.856	0.211
Water cover	-0.071	0.890
Bedrock	0.086	0.850
Elevation	-0.028	-0.919

I calculated the catch-per-unit-effort (CPUE) of Coeur d'Alene salamanders captured per survey, per stream and terrestrial area for each site (# per 100 m long stream site). I used CPUE to illustrate the relative abundance of Coeur d'Alene salamanders among sites within the stream and terrestrial habitats. In general, the CPUE = 0 sites were grouped together and there appeared to be a separation between the higher elevation sites without salamander detections and the lower elevation sites with a range of CPUE from 1 to 11 salamanders per night within the stream and terrestrial habitat types (Figs. 3.12-3.15).

Of the three factors describing the stream habitat among the study sites, only surface water (elevation, water cover, and bedrock) distinguished low CPUE sites from high CPUE sites. The factor scores for each study site were plotted along continuums representing how much of each factor a site has. On the geomorphology factor, sites scored throughout the continuum from -1.5 to 2.0 (Fig. 3.12). The lower elevation sites scored > 0 on the surface water factor and throughout the continuum on the bank gradient factor (Fig. 3.13). Higher elevation sites with intermittent stream flow and 0 to 2 CPUE were clustered close to 0 on the bank gradient factor and < 0 on the surface water factor (Fig. 3.13).

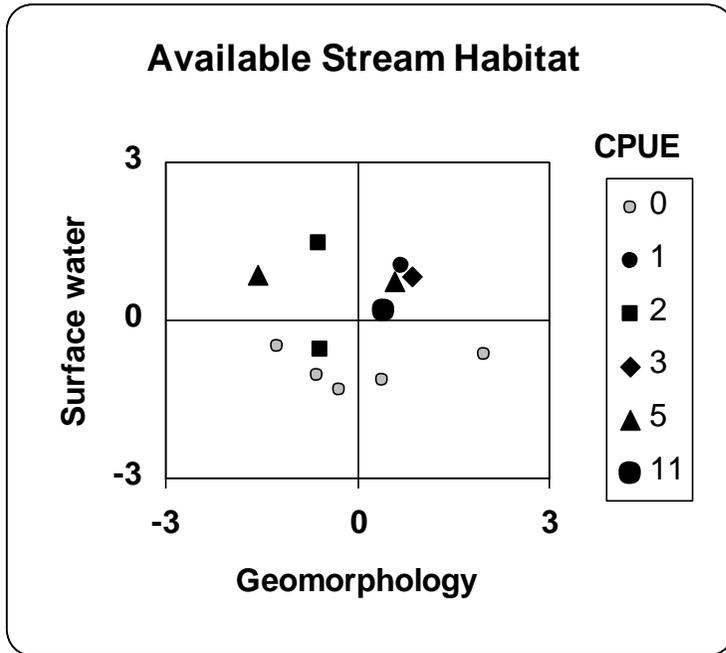


Figure 3.12: Available stream habitat site scores for factor 1 (geomorphology) and factor 2 (surface water) that differentiate habitat characteristics among 12 study sites on Mount Revelstoke, B.C. Factor scores for each site are based on a z-score scale ranging from -3.0 to + 3.0. Sites are coded by catch-per-unit-effort (CPUE), an indicator of relative abundance of Coeur d'Alene salamanders on the study sites in 2006.

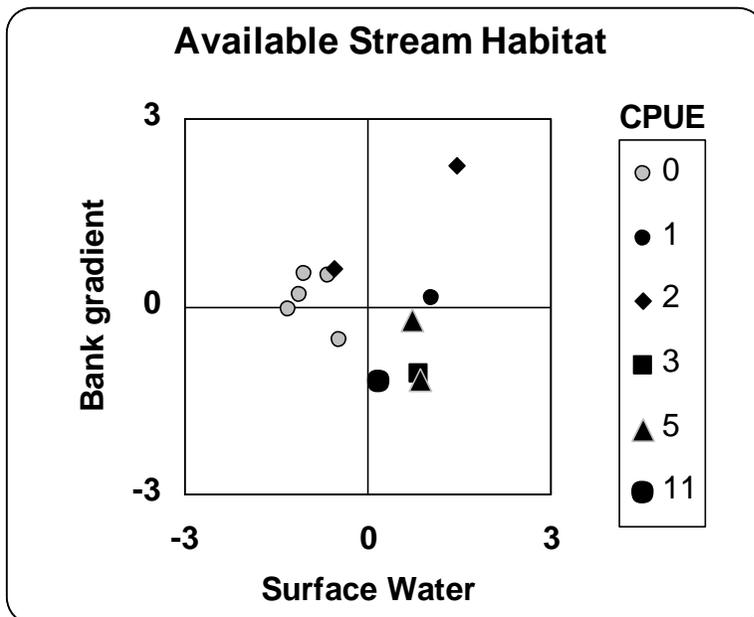


Figure 3.13: Available stream habitat site scores for factor 2 (surface water) and factor 3 (bank gradient) that differentiate habitat characteristics among 12 study sites on Mount Revelstoke, B.C. Factor scores for each site are based on a z-score scale ranging from -3.0 to + 3.0. Sites are coded by catch-per-unit-effort (CPUE), an indicator of relative abundance of Coeur d'Alene salamanders on the study sites in 2006.

3.4.2 Terrestrial habitat

Factor analysis was used to reduce and summarize the terrestrial habitat data into a small number of factors that accounted for correlations among the original variables. The original 21 continuous variables (Table 2.2) were reduced to nine variables and three explanatory factors that have biological meaning. The factor names were derived from the biological meaning of each variable group. Using the NFactor option and the Varimax rotation, three factors were kept based on the eigenvalues > 1 rule (Kaiser 1960).

Factor 1 represented the correlation between the substrate variables gravel, sand, and bare soil (Table 3.4). Factor 2 (ground cover) was correlated with elevation, shrub and forb cover, and litter cover (Table 3.4). Factor 3 (gradient) represented the correlation between the stream bank cover and quadrat gradient. The factor scores for each site were plotted along the continuum illustrating the amount of each factor a site has. The substrate continuum isolated one site (MON2) that scored very high (3.15) indicating this site has relatively more gravel, sand, and soil than the other 11 sites (Fig. 3.14). MON2 is a unique site where the stream exhibits a braided pattern over mixed rock and soil for 30 m. Ground cover divided the high elevation sites, which had more litter and shrub cover, from the lower elevation sites, which had relatively less ground cover (Fig. 3.14). The gradient factor illustrated that sites with 0 to 10 CPUE have a range of gradients in the terrestrial habitat (Fig.3.15).

Table 3.4: Three factor model resulting from exploratory factor analysis of terrestrial habitat variables that describe Coeur d'Alene salamander habitat along streams on Mount Revelstoke, BC. Values represent the correlation between each variable and each factor, also called factor loadings. Bold values indicate the variables that load primarily on a single factor, from which the factor descriptor (in parentheses) is derived.

	Factor 1 (Substrate)	Factor 2 (Ground cover)	Factor 3 (Gradient)
Gravel	0.996	-0.053	0.025
Sand	0.978	-0.101	-0.003
Soil	0.964	-0.142	-0.041
Elevation	-0.154	0.945	-0.020
Shrub cover	0.133	0.914	-0.205
Litter cover	-0.292	0.857	0.019
Left bank cover	0.015	0.072	0.956
Right bank cover	-0.211	-0.077	0.917
Quadrat gradient	0.172	-0.203	0.847

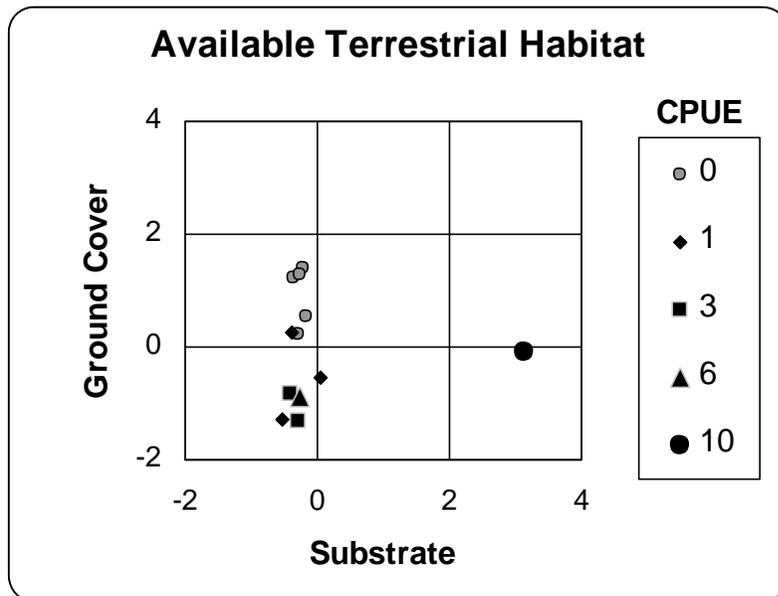


Figure 3.14: Available terrestrial habitat site scores for factor 1 (substrate) and factor 2 (ground cover) that differentiate habitat characteristics among 12 study sites on Mount Revelstoke, B.C. Sites are coded by catch-per-unit-effort (CPUE), an indicator of relative abundance of Coeur d'Alene salamanders on the study sites in 2006. Site MON2 scored high on all three substrate variables, gravel, sand, and bare soil.

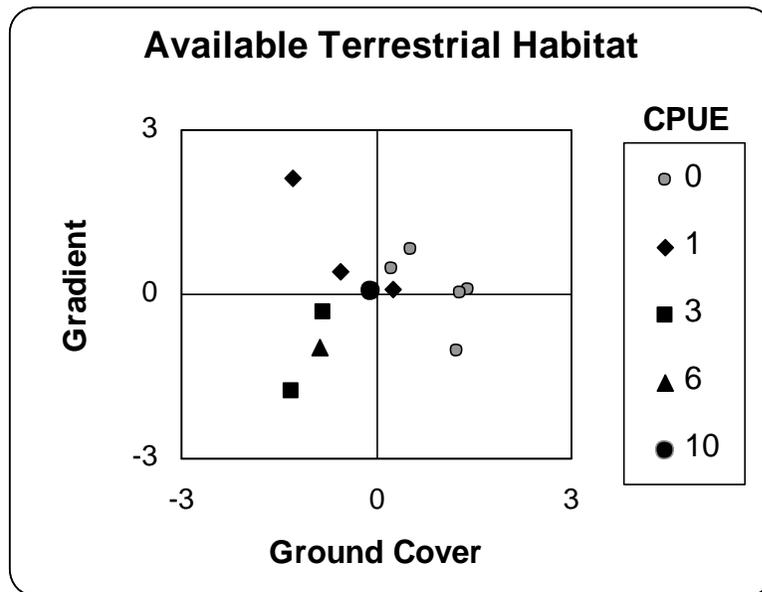


Figure 3.15: Available terrestrial habitat site scores for factor 2 (ground cover) and factor 3 (gradient) that differentiate habitat characteristics among 12 study sites on Mount Revelstoke, B.C. Sites are coded by catch-per-unit-effort (CPUE), an indicator of relative abundance of Coeur d’Alene salamanders on the study sites in 2006.

3.4.3 *Microhabitat associations*

3.4.3.1 **Stream habitat**

The global model was the best approximating model of nine logistic regression models explaining the microhabitat associations of Coeur d’Alene salamanders (Table 3.5). Salamander occupancy within stream habitat was positively associated with distance from stream centre, stream reaches (run versus underground), quadrat gradient, grass cover, litter cover, bryophyte cover, cobble, and boulders within the stream banks. Salamander stream plot occupancy was negatively associated with stream gradient, elevation, and water cover. The remaining eight models were not competitive in explaining salamander occupancy of stream plots ($\Delta AICc > 5.0$).

Table 3.5: Candidate models of Coeur d'Alene salamander stream microhabitat associations from logistic regression analysis. Stream variables were initially retained by the stepwise procedure using PROC LOGISTIC in SAS. Further fitting of the models required removal of variables based on maximum likelihood estimates > 0.05. AIC_c are Akaike units corrected for small sample size, -2LL is the -2 log likelihood, K is the number of parameters and n is the number of observations. Models are sorted by AIC_c.

Stream Models	Parameters	Percent concordant	-2LL	K	n	AIC _c	ΔAIC _c
Global	Intercept + S_dis + Htype(Run) - S_gra + Q_Gra - Elev + gcov - wcov + lcov + bcov + cobb + boul	88.4	247.2	13	284	274.5	0.0
Continuous Variables	Intercept + S_dis + Q_gra + gcov - wcov + cobb + boul + ccov + lcov + bcov	87.5	261.1	9	287	279.7	5.2
Literature	Intercept + S_dis - S_gra - wcov + Q_gra + cobb + ccov + boul + Htype(Riffle) + Htype(Run) - Htype(Step_pool) + RB_sub(DW_rock) - RB_sub(Litter) + LB_sub(Moss) + LB_cov(Shrub_forb)	89	243.1	22	290	290.9	16.4
Author's Observations	Intercept - wcov + Htype(Run) + Q_Gra + ccov + gcov + bcov + cobb	85.5	278.1	9	288	296.7	22.2
Past Studies	Intercept - wcov + RB_sub(Cobb) + RB_sub(DW_Rock) - RB_sub(Moss) + Q_gra + cobb + Htype(Run) - Htype(Step_pool) + ccov + boul	84.9	281.0	14	291	310.5	36.0
Cassirer and Groves (1994)	Intercept - wcov + cobb + Htype (Run) + ccov + boul	80.4	308.9	7	291	323.3	48.8
Stream Factor Analysis Variables	Intercept + Q_gra + boul - wcov - RB_gra + ccov	78.7	319.5	5	286	329.7	55.2
Gradient/Substrate	Intercept + Q_Gra - LB_sub(DW) + LB_sub(Litter) + RB_sub(Cobb) - RB_sub(DW) + cobb + boul + bcov + lcov	82.4	298.0	16	289	332.0	57.5
Substrate	Intercept - LB_sub(DW) + LB_sub(Litter) + RB_sub(Cobb) - RB_sub(DW) + cobb + boul + bcov + lcov	80.8	308.7	15	289	340.4	65.9

3.4.3.2 Terrestrial habitat

The global model was the best approximating model of eight logistic regression models explaining the microhabitat associations of Coeur d'Alene salamanders in the terrestrial habitat beyond the stream (Table 3.6). Salamander terrestrial plot occupancy was positively associated with stream gradient, quadrat gradient, quadrat aspect (up to 180 degrees), cobble in the stream bank and litter, shrub, and forb cover of the stream bank. Salamander terrestrial plot occupancy was negatively associated with low water volume, downed wood in and covering the stream bank, distance from stream centre, and elevation. The remaining seven models were not competitive in explaining salamander occupancy of stream plots ($\Delta AICc > 33.0$).

Table 3.6: Candidate models of Coeur d’Alene salamander terrestrial microhabitat associations from logistic regression analysis. Terrestrial variables were initially retained by the stepwise procedure using PROC LOGISTIC in SAS. Further fitting of the models required removal of variables based on maximum likelihood estimates > 0.05. AIC_c are Akaike units corrected for small sample size, -2LL is the -2 log likelihood, K is the number of parameters and n is the number of observations. Models are sorted by AIC_c.

Terrestrial Models	Parameters	Percent concordant	-2LL	K	n	AICc	ΔAICc
Global	Intercept - W_vol (Low) + LB_sub (Cobble) - LB_sub (DW) - RB_cov (DW) +RB_cov (Litter) + RB_cov (Shrub_forb) + S_gra - Elev - S_dis + Q_Gra + Q_ASP	86.3	212.87	17	233	249.71	0.0
Aspect/Gradient/Substrate	Intercept + Q_gra + Q_ASP + bed + grav + soil	74.4	272.86	5	239	283.12	33.4
Substrate/Cover	+ grav + RB_sub(Bed_boul)+ RB_sub(Cobble) - RB_sub(DW)	82.8	296.82	9	299	315.45	65.7
Gradient/Substrate/Cover	Intercept + Q_gra + grav + soil + ccov + gcov + bcov + boul	81.6	301.62	7	290	316.02	66.3
Terrestrial Factor Variables	Intercept + grav - lcov + Q_gra - shcov	77.7	321.23	4	286	329.37	79.7
Factor Analysis Variables	Intercept + grav - shcov + Q_gra	74.3	330.98	3	286	337.07	87.4
Cassirer and Groves (1994)	Intercept + wcov + S_gra + Q_gra - LB_sub(Bed_boul) + LB_sub(Litter) + RB_sub(Bed_boul) + RB_sub(Cobble) - RB_sub(DW)	80.2	315.72	12	292	340.84	91.1
Stepwise of all Variables	Intercept +RB_sub (Bed_boul) + RB_sub(Cobble) - RB_sub(DW) + wcov + grav	71.8	331.77	7	309	346.14	96.4

4 DISCUSSION

Coeur d'Alene salamanders, classified as a species of special concern (COSEWIC 2001), occur along perennial stream reaches in the Thompson Moist Warm Interior Cedar-Hemlock variant (Braumandl & Curran 1992) on Mt Revelstoke. This study of Coeur d'Alene salamanders was conducted in Mount Revelstoke National Park, Canada with preliminary presence/no-detection surveys conducted north and east of the park boundary. Coeur d'Alene salamanders were captured throughout the length (75-100 m) and width (up to 5 m beyond the stream margin) of the study sites. Capture-mark-recapture efforts yielded a very low recapture rate, confounding efforts to estimate population abundance. Coeur d'Alene salamanders were more abundant below 950 m than at higher elevation sites. Sites below 950 m had more water and bedrock in the stream bed and less shrub, forb, and litter cover in the terrestrial area than sites above 950 m. Exposed, fractured bedrock appears to be an important habitat feature within streambeds as well as at waterfall and roadside seepage sites, as previously observed by others. The abundance, distribution, and microhabitat use of Coeur d'Alene salamanders appears to be associated with temperature, proximity to water, and availability of bedrock, boulder, and cobbles.

4.1 SALAMANDER RELATIVE ABUNDANCE

Relative abundance of Coeur d'Alene salamanders was lower on study sites along streams on Mt. Revelstoke (0.034 ± 0.009 per m^2) than at waterfall and roadside seepage sites surveyed with similar methods (0.18 ± 0.19 per m^2) along the Columbia River valley north of Revelstoke, B.C. (Ohanjanian 2001). Standardized counts were also lower along these study streams compared to other eastern and western *Plethodon* species in the

literature. A comparison to *Plethodon cinereus* is provided here because a range of count data was available in the literature for this extensively studied eastern *Plethodon* using non-destructive nocturnal survey methods as used in this study. Coeur d'Alene salamanders occurred at an average abundance of 0.0013 per m² (970 m) to 0.034 per m² (600-800 m) in this study, which was lower than counts of *P. cinereus* done with surface sampling on rainy nights (0.089-0.237 per m²; Burton & Likens 1975, 0.1-0.43 per m²; Grover 1998). A variety of alternative methods have been used to enumerate *P. cinereus*, including removal sampling (0.048 per m²; Test & Bingham 1948) or intensive surface litter and cover object sampling (0.3-1.3 per m²; Harper & Guynn 1999, 0.57 per m²; Messere & Ducey 1998, 0.8-4.0 per m²; Jaeger 1979). Studies of species with similar habitat associations to Coeur d'Alene salamanders used more intensive survey methods, including vegetation removal and downed wood excavation, and provided indices of abundance (Wilkins & Petersen 2000, Vesely & McComb 2002) that are not directly comparable to the results of this study.

Researchers caution against using count data, unadjusted for detection probabilities, to compare population parameters (Dodd & Dorazio 2004; Schmidt 2004) among species, sites or time periods because the probability of detecting individuals may vary with species, individuals, survey method, vegetation cover, previous and current weather conditions, season, reproductive strategy and age class (Taub 1961, Grover 1998, Petranka & Murray 2001, Bailey et al. 2004, Dodd & Dorazio 2004). In this study, Coeur d'Alene salamander surveys were conducted by a consistent team of observers, repeating the same methods. There was no evidence of high site capture rates related to rainfall events on the day of the survey or the immediate days prior. Although the highest densities of salamanders occurred on nights with wet substrate, high counts were also recorded during dry substrate conditions.

During salamander surveys of MON3 (relative abundance = 0.0013 per m²) ambient air temperature was 10°C, within the range preferred by *P. jordani*, *P. ouachitae*, *P. glutinosus*, and *P. cinereus* (Taub 1961; Spotila 1972). Temperature is a limiting factor in *Plethodon* surface activity (Taub 1961) and the highest abundance of salamanders in this study occurred with air temperatures from 6°C-12°C. Incorporating environmental covariates in population estimates and detection probabilities has been recommended; however, this study did not detect a simple relationship between environmental variables and Coeur d'Alene salamander surface abundance.

4.2 SPATIAL DISTRIBUTION

The results of this study show that Coeur d'Alene salamanders occur along small perennial stream reaches from 560 m to 980 m in the Thompson Moist Warm Interior Cedar-Hemlock (ICH mw3) variant (Braumandl & Curran 1992) on Mt. Revelstoke. Once salamanders were detected at one location on a stream, they were also found along the same stream channel on randomly located sites, indicating that occurrences are not isolated along the elevation gradient of a perennial stream.

Coeur d'Alene salamanders occur in dry, moist, and wet climatic regions from northern Idaho to southeastern British Columbia (Wilson 1991, Ohanjanian 1999). The northern-most occurrence of Coeur d'Alene salamanders occurs in the Wells Gray Wet Cool Interior Cedar-Hemlock (ICHwk1) variant, near the mouth of Goldstream River, 95 km north of Revelstoke, B.C. The upper elevation (987 m) of salamander occurrences on Mt. Revelstoke corresponds roughly with the transition from the Interior Cedar-Hemlock zone to the Engelmann Spruce-Subalpine Fir zone, in a similar fashion to the distribution of the closely related *Plethodon vandykei* in western Washington (Wilson et al. 1995) and Coeur

d'Alene salamanders in the United States (Wilson & Larsen 1998). There is a thin strip of ICHwk1 between the highest salamander location and the subalpine forest on the southwest face of Mt. Revelstoke, suggesting that Coeur d'Alene salamanders could occupy available habitat there based on climate variables (annual average precipitation, growing degree days 5°C) and underlying geological material.

The absence of water in streambeds during the summer months appears to be an important limiting factor on the higher elevation sites. In the drier region surrounding the Kootenay/Koocanusa watershed, Coeur d'Alene salamanders occur in close association with surface water, either along v-shaped creeks or seepage on rock walls up to 1234 m (Ohanjanian 2000). In this study, a high proportion of stream centre plots 49% (82/166) were classified as having underground water flow. These quadrats were dry in late August or had water flowing under organic deposits of soil and vegetation. Of these, 65% (53/82) were on streams with intermittent flow (dry streambed in late August) where no salamanders were detected.

4.2.1 Site level distribution

Salamanders were detected from the stream margin out to the 5 m boundary of the search area on all detected sites, suggesting that Coeur d'Alene salamanders are distributed along stream edges similar to semi-aquatic *Desmognathus* species (Hairston 1949). Coeur d'Alene salamanders were found closer to water in August ($64\text{ cm} \pm 9.1\text{ SE}$) compared to June ($173\text{ cm} \pm 23.25\text{ SE}$) and used the streambed habitat more often relative to terrestrial habitat during the warm and dry weather in August. Plethodontid salamanders occur within a range of environmental conditions (Spotila 1972, Feder 1983, Grover 2000). Proximity to water and relatively cool and moist substrate is likely an example of Coeur d'Alene

salamanders' preference for moisture within a gradient of environmental conditions. Coeur d'Alene salamanders may have a similar dehydration rate to the semi-aquatic species *D. monticola* and *D. fuscus* that are found closer to water (112 cm and 118 cm), respectively, than the terrestrial salamanders *P. cinereus* and *P. glutinosus*, which were found an average of 1095 cm and 1130 cm from water respectively during night surveys (Grover 2000). As with *D. monticola*, Coeur d'Alene salamanders may be exhibiting an ecological preference for terrestrial habitat that is in close proximity to water and is high in humidity, compared to streambed substrate (Hairston 1949), especially during long periods without precipitation.

The proportion of adults in June 2006 (0.68) and August 2006 (0.81) was weighted higher in this study than the adult proportion reported by Lynch (1984) in June (0.58) and August (0.60) in his intensive study of the reproductive ecology of Coeur d'Alene salamanders in Idaho. However, we observed neonates in June, July, and August while Lynch (1984) reported the last neonates of the season in June. Neonate, juvenile, and adult salamanders were observed throughout the study sites in June and August 2006. The change in proportion of neonates: juveniles: adults between June (0.13: 0.2: 0.67) and August (0.02: 0.17: 0.81) indicated a decrease in juveniles with a corresponding increase in adults over the summer, which may be explained by juveniles maturing into adults. Lynch (1984) recorded very little change in the age class distribution within a population of Coeur d'Alene salamanders at Elk Creek Falls, Idaho between June (0.06: 0.36: 0.58) and August (0: 0.4: 0.6) 1980. Lynch (1984) also recorded variation in the relative proportion of age classes in the same month across years, suggesting several years of data may be required to reveal seasonal patterns. Juvenile and adult Plethodontid salamanders may respond to changes in environmental conditions differently; juveniles may retreat from the surface during dry

conditions to conserve moisture while adults may still be active on the surface (Grover 1998).

4.3 HABITAT

The three streams in this study flow through a cedar-hemlock forest over a metamorphic complex of unconsolidated morainal deposits (Achuff et al. 1984). Our results are consistent with the biogeographic analysis of Wilson & Larsen (1998) in that Coeur d'Alene salamanders occur in coniferous forest with > 50 cm average annual precipitation below 1100 m elevation. All three streams flow over the same general southwestern aspect of Mt. Revelstoke. Coeur d'Alene salamanders occur along streams with a mixture of rock and soil, exposed bedrock, and a water table high enough to provide water at the surface throughout the summer season. The presence of exposed bedrock or mixed rock and soil on sites with salamanders is consistent with other researchers' observations of Coeur d'Alene salamander habitat (Slater & Slipp 1940, Nussbaum et al. 1983, Lynch 1984, Wilson & Larsen 1988). Coeur d'Alene salamanders occupy sites in unconsolidated material in the northern part of its range, while southern populations of this species occur in association with consolidated materials (Wilson & Larsen 1998).

4.3.1 *Microhabitat*

Previous surveys in the United States and southeastern British Columbia have determined that Coeur d'Alene salamanders reside in a variety of habitats from rock faces, perennially wet from the splash of a waterfall, to intermittent seeps, mixed rock and soil talus, and streamside habitat (Slater & Slipp 1940, Teberg 1965, Lynch 1984, Nussbaum et al. 1983, Wilson et al. 1989, Groves et al. 1996). The primary objective of previous surveys

for Coeur d'Alene salamanders was to establish the geographic range of the species and to describe the distribution of populations within that range (Groves 1988, Wilson 1990, Wilson 1991, Ohanjanian 1997, Ohanjanian 1999, Ohanjanian 2000, Ohanjanian 2001). Past surveys and studies of Coeur d'Alene salamanders focused on waterfall or seepage habitat, roadside seepages being the easiest to access (Lynch 1984, Wilson & Larsen 1988, Lindeman 1993, Ohanjanian 2001).

This research provides insight into salamander microhabitat associations within stream habitats at a finer spatial scale than previously discussed in the published literature. The odds are higher for Coeur d'Alene salamander occurrence away from stream centre within streambeds and closer to stream centre in terrestrial habitat. Within streambeds, salamander occurrence was associated with ground cover vegetation in low gradient reaches, with retreat features like cobble and boulders present. Vegetation within a streambed may offer greater moisture retention at the surface during low water conditions. Within terrestrial habitats, stream bank features offering vegetative cover (forbs and shrubs) may result in lower temperatures and decreased water loss from solar radiation during the day to the extent that salamanders can detect a moisture gradient on the surface during their nocturnal foraging activities.

Logistic regression analysis reflected the importance of habitat features identified in the site level analysis (surface water, gradient, boulders, shrub cover, forb cover) in addition to finer scale features (cobble, moss, grass) that combined, describe retreat characteristics and habitat moisture preferences of Coeur d'Alene salamanders. Shrubs, forbs, and moss were associated with salamander occurrence on the surface compared to randomly available plots in this study. This is similar to the findings of Petranka and Murray (2001), who found

higher abundance of terrestrial *Plethodon* and *Desmognathus* species with greater vegetation cover. Grover (1998) found that increasing the density of cover objects in experimental field plots resulted in an increase in both adult and juvenile *Plethodon cinereus* and *P. glutinosus*.

Plethodontid salamanders accommodate their physiological requirement for moisture (Spotila 1972, Feder 1983, Petranka et al. 1993, deMaynadier and Hunter 1998) through moisture-conserving strategies such as nocturnal surface activity, use of cover objects or natural retreats, and proximity to water. In most cases, we captured salamanders fully or partially exposed on the surface. On four occasions, we captured salamanders under a cover object and approximately 50% of all captured salamanders retreated “under” rock, downed wood, tree roots, or litter when released, indicating that cover objects are likely important for escape from predators.

4.4 FUTURE RESEARCH

This study showed that Coeur d’Alene salamanders are dispersed along small perennial streams within a narrow elevation gradient limited by climatic conditions or lack of surface water. Future work is needed to determine how far this species is distributed along a horizontal gradient away from wet streambeds. Are individuals dispersing between streams when the water sources are less than 50 m apart? Does dispersal only occur on warm rainy nights? Future work could explore the question of how the degree of isolation between populations varies between habitat types and climatic zones throughout the species’ range since this is one of the key factors that make Coeur d’Alene salamanders a Species at Risk in Canada.

Further study could investigate what factors improve or decrease the probability of detecting this species at the site level and the landscape scale. Researchers have developed standardized methods for surveying salamanders (Heyer et al. 1994) and biometricians have developed sampling and counting methods that take into consideration detection probabilities, a necessary step to improve abundance estimates (MacKenzie et al. 2002, Pollock et al. 2002, Bailey et al. 2004). Although improved sampling methods and statistical theory have been developed for estimating population parameters of abundant populations, these tools often do not transfer over easily to difficult-to-detect species (Thompson 2004).

5 CONCLUSION

In this study, Coeur d'Alene salamanders occurred between 600 m and 980 m within the Interior Cedar-Hemlock forest on Mt. Revelstoke, BC. Beyond the Mount Revelstoke National Park boundaries, the low order stream habitat of this species is subject to disturbance from forestry, mining, road building, road maintenance, and watercourse diversions, such as "run-of-the-river" hydro projects. Coeur d'Alene salamanders appear to spend much of their time underground and the results of this study indicate that they may occur in forests subject to disturbance without ever being detected due to their nocturnal activities.

Coeur d'Alene salamanders are challenging to enumerate due to their probable vertical distribution within the morainal material underlying the cedar-hemlock forest and the natural cover of rock, soil and litter on the forest floor. This challenge may be best addressed with an adaptive management approach to monitoring the species in optimal habitat (Thompson 2004) within the protected area of the National Park, concurrently with studying sites subject to disturbance (Welsh et al. 2008) to determine how Coeur d'Alene salamanders respond. An adaptive management approach can incorporate information at various spatial scales, including occupancy modelling and testing to monitor changes in spatial distribution with changes in water sources from stream development, water table draw downs, and climate change. As more is learned about this elusive species, this can be incorporated into ongoing monitoring efforts.

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APPENDIX: Coordinates of Coeur d’Alene salamander survey locations

Location	Site Name	UTM 11 NAD 83		Habitat	Elevation (m)	No. Surveys ¹		Salamanders observed?
		Northing	Easting			Detection	No Detection	
North N1	N19	417381	5657427	Waterfall	591	0	2	N
North N2	N17 ²	416942	5656329	Stream	620	1	0	Y
North N3	Revelstoke Dam ³	416226	5655550	Waterfall	563	2	0	Y
MRNP 1	5KA	416153	5651505	Waterfall	577	11	1	Y
MRNP 2	5KC	415907	5652671	Stream	658	0	2	N
MRNP 3	Site 12 ⁴	416372	5652091	Stream / Waterfall	748	0	1	N
MRNP 4	Double Falls ⁵	416998	5651365	Waterfall	811	1	0	Y
MRNP 5	Monashee Lookout	416852	5651567	Stream	844	1	1	Y
MRNP 6	5KB1	415873	5651969	Stream	597	5	1	Y
MRNP 7	5KB2	416048	5652200	Stream	682	6	0	Y
MRNP 8	5KB3	417026	5652742	Stream	1093	0	4	N
MRNP 9	5KB4	417247	5652950	Stream	1204	0	5	N
MRNP 10	DBF1	416695	5651035	Stream	646	5	1	Y
MRNP 11	DBF2	417004	5651192	Stream	760	6	0	Y
MRNP 12	DBF3	418100	5652217	Stream	1254	0	3	N
MRNP 13	DBF4	418139	5652370	Stream	1312	0	4	N

¹ Average person minutes per survey was 25 min

² Surveyed with no detections in 2001 (P. Ohanjanian, personal communication, February 15, 2006)

³ Surveyed with salamanders detected in 2001 (P. Ohanjanian, personal communication, February 15, 2006)

⁴ Surveyed in 2003 and 2004 with no detections (Dykstra 2004, Adama and Ohanjanian 2005)

⁵ Surveyed in 2003 resulting in the first detections of Coeur d’Alene salamanders in MRNP (Dykstra 2004)

Location	Site Name	UTM 11 NAD 83		Habitat	Elevation (m)	No. Surveys ¹		Salamanders observed?
		Northing	Easting			Detection	No Detection	
MRNP 14	MON1	416864	5651166	Stream	719	6	0	Y
MRNP 15	MON2	416941	5651343	Stream	768	12	1	Y
MRNP 16	MON3	417023	5651977	Stream	962	4	3	Y
MRNP 17	MON4	417411	5652451	Stream	1196	0	6	N
MRNP 18	Bridge Creek	418862	5652368	Stream	1350	0	2	N
MRNP 19	Snow Forest	417923	5652671	Stream	1090	0	4	N
East 1	Water Tower	416391	5650746	Stream	530	0	1	N
East 2	Eastern Access West	416391	5650435	Stream	550	0	1	N
East 3	Water Main	420695	5650185	Stream	537	0	1	N
East 4	Hamilton Creek	420695	5652900	Stream	649	0	1	N

¹ Average person minutes per survey was 25 min