THE HABITAT ECOLOGY OF THE POST-METAMORPHIC COASTAL TAILED FROG (*Ascaphus truei*)

by

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ABSTRACT

The coastal tailed frog (*Ascaphus truei*) has a biphasic life-history that includes the use of high-elevation streams and adjacent old growth forests. This species is at risk from a variety of land-use activities that result in younger and more fragmented terrestrial habitats. I investigated the fine-scale spatial ecology of post-metamorphic tailed frog populations as revealed by seasonal variation in activity and movement. I used an Information Theoretic Model Comparison approach to relate tailed frog captures in pitfall traps to sets of explanatory factors and infer habitat use by adult tailed frogs located with VHF radio transmitters. Trap data suggested that variation in the relative abundance and distribution was attributed to time of year, associated with reproductive activity; seasonal trends in local climate; canopy closure; and distance to the larval stream. The most parsimonious logistic regression model for both years of trapping data demonstrated 'good' predictability (Area Under the Curve (AUC) > 0.7). Data from 24 tailed frogs with radio transmitters (8 males, 16 females) fitted to a resource selection function suggested that tailed frogs were positively associated with habitats containing decayed coarse woody debris (CWD), less light, adjacency to the larval stream, wet site types, and cool temperatures (11-12° C). When compared to males, females were more selective in their choice of habitat (AUC > 0.7). Overall, the relationship between distribution and activity of tailed frogs was reflective of reproductive phenology in combination with micro-site or broader climatic conditions. Thus, habitat protections should reflect the behavior and habitat of the species as it varies across spatiotemporal scales.

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CHAPTER 1

GENERAL INTRODUCTION

INTRODUCTION

Species Distribution

The tailed frog genus, *Ascaphus,* is endemic to the Pacific Northwest of North America and inhabits the cold-flowing streams associated with those forests (Brown 1975; Wallace and Diller 1998; Bury and Adams 1999; Ritland *et al.* 2000; Wahbe et al. 2004; Matsuda and Richardson 2005; Hayes *et al.* 2006). There are 2 species within North America, *Ascaphus montanus* and *A. truei*. These species occupy environmental regimes extending from the drier, colder climate found in the interior Rocky Mountains (*A. montanus*; Daugherty and Sheldon 1982) to the wet climate along the Pacific coast (*A. truei*; Bury 1968). The range of *A. truei* extends from northwestern California to the Nass River, north of Prince Rupert, British Columbia (BC; Dupuis and Bunnell 1997). The range of *A. montanus* is more interior from southeastern BC and southeastern Washington into south-central Idaho and northeastern Oregon (Leonard *et al.* 1993; Nielson *et al.* 2001; Stebbins 2003).

Species Ecology and Biology

Past research on the biology and ecology of *A. truei* has focused on the larval life stage (Bury and Adams 1999; Dupuis and Steventon 1999; Wahbe and Bunnell 2001; Hayes *et al.* 2006; Karracker *et al.* 2006; Burkholder and Diller 2007). As such, this species is known to be associated with mountainous lotic environments flowing through old-growth stands containing a well-vegetated understory (Green and Campbell 1984). Under laboratory conditions, Brown (1975) reported that for healthy embryonic development streams must maintain temperatures from 5-18.5°C; however, temperatures in more northerly climates may exceed this minimum during the winter. Larvae can take 1-4 years to fully metamorphose, but the variation in timing is reflective of the geographic range of this species (Bury and Adams 1999).

Ascaphus are the longest-lived anuran (15-20 years) and reach sexual maturity at 8-9 years (Daugherty and Sheldon 1982; Brown 1990). Breeding occurs in early fall (September to October) depending on the geographic location (Green and Campbell 1984). The genus has evolved internal fertilization as a reproductive strategy because breeding occurs in flowing streams or small pools close to larval streams (Green and Campbell 1984; Bull and Carter 1996; Ritland *et al.* 2000). Clutch sizes for *A. truei* range from 44-85 eggs deposited in double strands under rocks in cool-flowing streams (Karracker *et al.* 2006) from late June to early July following the fall breeding.

Post-metamorphic *A. truei* are sensitive to ambient air temperature > 24°C and, relative to many other anurans, are less tolerant of desiccation, which may limit movement across dry or warm terrestrial environments (Claussen 1973a; Brown 1975; Daugherty and Sheldon 1982). Additionally, multiple studies have demonstrated that tailed frogs are extremely philopatric to reproductive streams (Daugherty and Sheldon 1982; Wahbe *et al.* 2004; Matsuda and Richardson 2005; Burkholder and Diller 2007). However, juveniles have been identified traveling up to 100 m from larval streams, leading researchers to hypothesize that this age class is responsible for emigration (Daugherty and Sheldon 1982; Wahbe *et al.* 2004).

Conservation Issues

Ascaphus have specialized life-stage requirements resulting in an inherent vulnerability to anthropogenic and natural disturbances that may influence the quality or availability of habitat. As a result, the tailed frog has been designated as a Blue Listed species by the BC Conservation Data Centre (CDC) and has been listed as Special Concern under the federal Species at Risk Act (SARA). Within BC, anthropogenic disturbances that remove forest overstory and reduce the complexity of downed and standing wood in the understory have the potential to reduce the distribution or productivity of populations of the tailed frog (Dupuis and Waterhouse 2001).

Some researchers in North America suggest that the decline in amphibian abundance is associated with clearcut or shelterwood logging (Olson *et al.* 2007; Kluber *et al.* 2008; Hawkes and Gregory 2012). Factors associated with forest harvesting and the decline of tailed frogs include the loss of complex structural components in maturing or old forests, such as coarse woody debris; reduction of overstory cover; and changes in hydrological processes (Dupuis and Waterhouse 2001). For example, Hawkes and Gregory (2012) in Washington State, United States of America (USA), demonstrated that the relative abundance of tailed frogs was generally higher in habitats upland of streams prior to logging. Additionally, Wind (2009) suggested southeastern populations of the tailed frog have been impacted by past dam and water construction around Lillooet BC, which may have interrupted migration pathways.

Conservation Management

Under the Forest and Range Practices Act (FRPA; formerly Forest Practices Code), the Identified Wildlife Management Strategy (IWMS) recognises two categories of wildlife that require special management or habitat protection: 1) Species at Risk; and 2) Regionally Important Wildlife. The coastal tailed frog is designated as a Species at Risk because of habitat requirements that are not protected under the FRPA and the documented effects of timber harvest on tailed frog populations. The tailed frog is associated with structural stages of mature (100-140 years) or old (> 140 years) forests and can be found along S4-S6 streams (small fish or non-fish bearing streams). Currently, these streams have fewer restrictions on anthropogenic activities, such as forestry.

As an identified wildlife species (IWMS) some habitat conservation exits in areas designated as ecological reserves, Wildlife Habitat Areas (WHAs), old growth management areas (OGMAs), or through the creation of special resource management zones for other species such as the grizzly bear. Additionally, certain management guidelines have been created for reserves designed for *A. truei*. For instance, around areas that contain tailed frogs, OGMAs or WHAs can be established to protect stands in serial stages 6 and 7. Boundaries of these reserves should contain a 30-m core area and have a 20-m management zone on both sides of the stream to reduce risk of windthrow and to maintain microclimate conditions and important structural elements (i.e., coarse woody debris) similar to an unaltered stand.

Previous Post-metamorphic Research

Past research on *Ascaphus* has focused on interior rocky mountain and southern populations (Daugherty and Sheldon 1982; Wahbe *et al.* 2000, 2004; Matsuda and Richardson 2005; Hayes *et al.* 2006; Burkholder and Diller 2007; Hawkes and Gregory 2012) with less work at their northern extent (Dupuis and Steventon 1999). Given the observed declines of southern populations following anthropogenic disturbances (Hawkins *et al.* 1988; Bull and Carter 1996; Hawkes and Gregory 2012), there is concern that tailed frogs at the northern extent of their distribution may also be negatively affected by activities such as forest harvesting, stream diversion, or the creation of linear corridors. However, the possible impacts are speculative as our knowledge of habitat requirements for the terrestrial life-stage of the species is limited.

Researchers investigating the movement and distribution of post-metamorphic *A. truei* have relied on data collected using pitfall traps (Wahbe *et al.* 2004; Matsuda and Richardson 2005; Hawkes and Gregory 2012) or area-constrained searches (Hayes *et al.* 2006; Burkholder and Diller 2007). However, recaptures are low for *A. truei* providing limited understanding of the spatial distribution of the population or the movement of individual tailed frogs. A better understanding of adult tailed frogs' ecology and biology is necessary to predict, monitor, and prevent or mitigate potential impacts resulting from habitat alteration and disturbance (Deguise and Richardson 2009).

Radio telemetry provides information describing animal movement that is not available by other methods (Bartelt and Peterson 2000). Historically, the size and weight of the transmitter has prevented the use of radio telemetry for monitoring movements and distribution of small amphibian species (Forsythe *et al.* 2004). However, advances in technology, such as the miniaturization of batteries, have resulted in an opportunity to apply this technique to small cryptic species like the tailed frog.

Radio-telemetry locations can be coupled with powerful statistical models to quantify movement dynamics, distribution, and habitat use (Rowley and Alford 2007). Resource selection functions (RSF) are one type of statistical model that use animal locations to quantify a species' distribution and habitat requirements (Johnson *et al.* 2004). A RSF compares the type of used resources or habitat at an animal location with those resources that are available (Manly *et al.* 2002). Quantifying and mapping species-habitat relationships can guide reserve design or inform land management activities (Boyce *et al.* 2002; Araujo *et al.* 2004; Cabeza *et al.* 2004; Koper and Manseau 2010).

Research Purpose

The goal of my thesis is to quantify the seasonal movement and habitat selection patterns of a northerly population of the tailed frog across a range of forest conditions modified by timber harvesting. These findings will broaden our understanding of the ecology and life history of the species within landscapes currently subjected to forestry and other land-use activities. The outcome of this study will guide the protection, management and restoration of headwater streams associated with tailed frog populations. Within the scope of my thesis, I addressed 3 research objectives:

(1) I used systematic pitfall data to summarise capture rates by demographic, temporal, environmental and treatment variables suspected to influence abundance and distribution.

(2) I used locations from tailed frogs monitored with radio telemetry to develop RSFs that quantified the distribution and habitat selection of tailed frogs.

(3) I employed radio telemetry and systematic pitfall traps to reveal temporal and environmental patterns in the movement of tailed frogs.

My thesis is structured as 4 chapters. In Chapter 1, I provide a general introduction to the study species, research objectives, and the study area. Researchers have observed that southerly populations of *A. truei* make seasonal large-scale movements that are dependent on life-history requirements. Furthermore, those movements and ultimately population distribution may be influenced by environmental conditions that act as a physiological or ecological constraint (Matsuda and Richardson 2005; Hayes *et al.* 2006). Thus, in Chapter 2, I used pitfall capture data and an Information Theoretic Model Comparison (ITMC) approach to test hypotheses predicting the distribution of populations of tailed frogs within a site relative to temporal, environmental, and treatment variables.

In Chapter 3, I used radio-telemetry data to identify the temporal and environmental factors that influence the movement, and resource selection of individual tailed frogs. Pitfall-trap data have limited utility for addressing such questions as movement and distribution are premised on recaptures, which are low for this species (Maxcy 2000; Wahbe et al. 2004; Matsuda and Richardson 2005; Hayes *et al.* 2006). This is the first study to use radio telemetry to quantify movement and resource selection of *Ascaphus* spp. Lastly, in Chapter 4 I summarize my findings, including a discussion of the conservation relevance and management applications of the research.

Study Area

My research occurred in 3 watersheds in the Hazelton Mountains centered on the Skeena River. These mountains are located on the leeward side of the Coast Mountains and are typically round-topped or domed ridges with small remnant glaciers that were created during the last ice age. Vegetation communities of the study area are representative of the transition between the Coastal Western Hemlock (CWH) and the Interior Cedar-Hemlock (ICH) biogeoclimatic zones.

The CWH zone is found along the coast from sea level to 1050 m on the leeward side of the mountains and has relatively mild temperatures and heavy rainfall (Figure 1). Mean annual temperatures can range from 5.2-10.5°C.

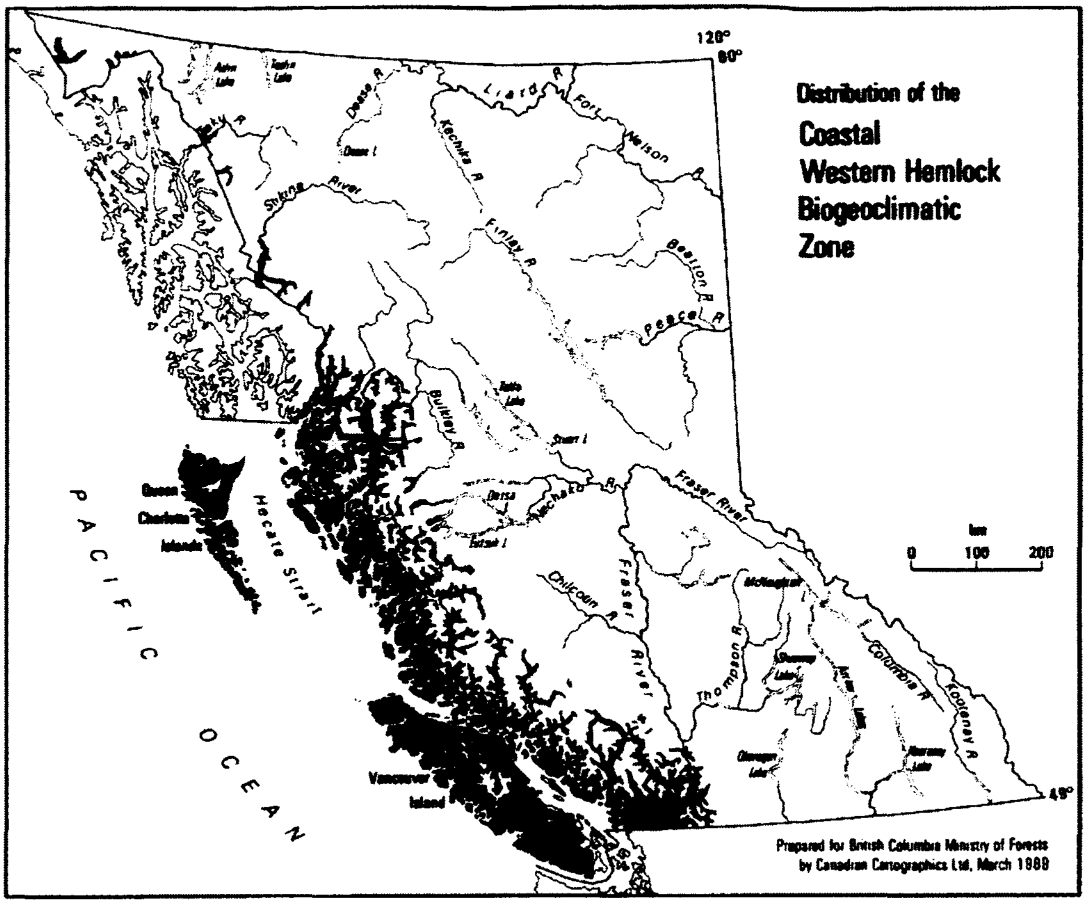

Figure 1: Distribution of the Coastal Western Hemlock Biogeoclimatic Zone in British Columbia. Figure from Meidinger and Pojar (1991). Grey star indicates location of research site.

The mean annual precipitation for this region is 2228 mm, approximately 40-50% of which is snowfall at the northern extent of the zone (Pojar *et al.* 1991).

Within the CWH, my study sites occurred in the wet submaritime subzone (CWHws). This subzone has some of the largest conifers in BC and has a dominant overstory consisting of western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*) and amabilis fir (*Abies amabilis*). The shrub layer contains Alaskan blueberry (*Vaccinium alaskaense*), oval-leaved blueberry (*V. ovalifolium*) and false azalea (*Menziesia ferruginea*). Common species in the herbaceous layer include queen's cup (*Clintonia uniflora*), one-sided wintergreen (*Orthilia secunda*), bunchberry (*Cornus canadensis*), twinflower (*Linnaea borealis*) and rattlesnake plantain (*Goodyera oblongifolia*). Typically, there is a well-developed moss layer that contains such species as red-stemmed feathermoss (*Pleurozium schreberi*), lanky moss (*Rhytidiadelphus loreus*), shaggy moss (*R. triquetrus*) and pipecleaner moss (*Rhytidiopsis robusta*; Pojar *et al.* 1991).

The ICH zone is located at lower to mid-elevations (100-1000 m), in a small pocket located east of the Coast Mountains in adjacent parts of the Hazelton Mountains (Figure 2). The continental climate produces cool wet winters and warm dry summers. The average range of temperatures is 2-8.7°C and annual mean precipitation is 500-1200 mm with approximately 25-50% being snow (Meidinger and Pojar 1991).

The most northern subzone is the ICHmc and refers to the 'moist and cold' climate found from Hazelton to Meziadin Lake. The climax over-story is dominated by conifers including western hemlock, western redcedar, Roche spruce (*Picea* x *lutzii*) and subalpine fir (*Abies lasiocarpa*; Meidinger and Pojar 1991).

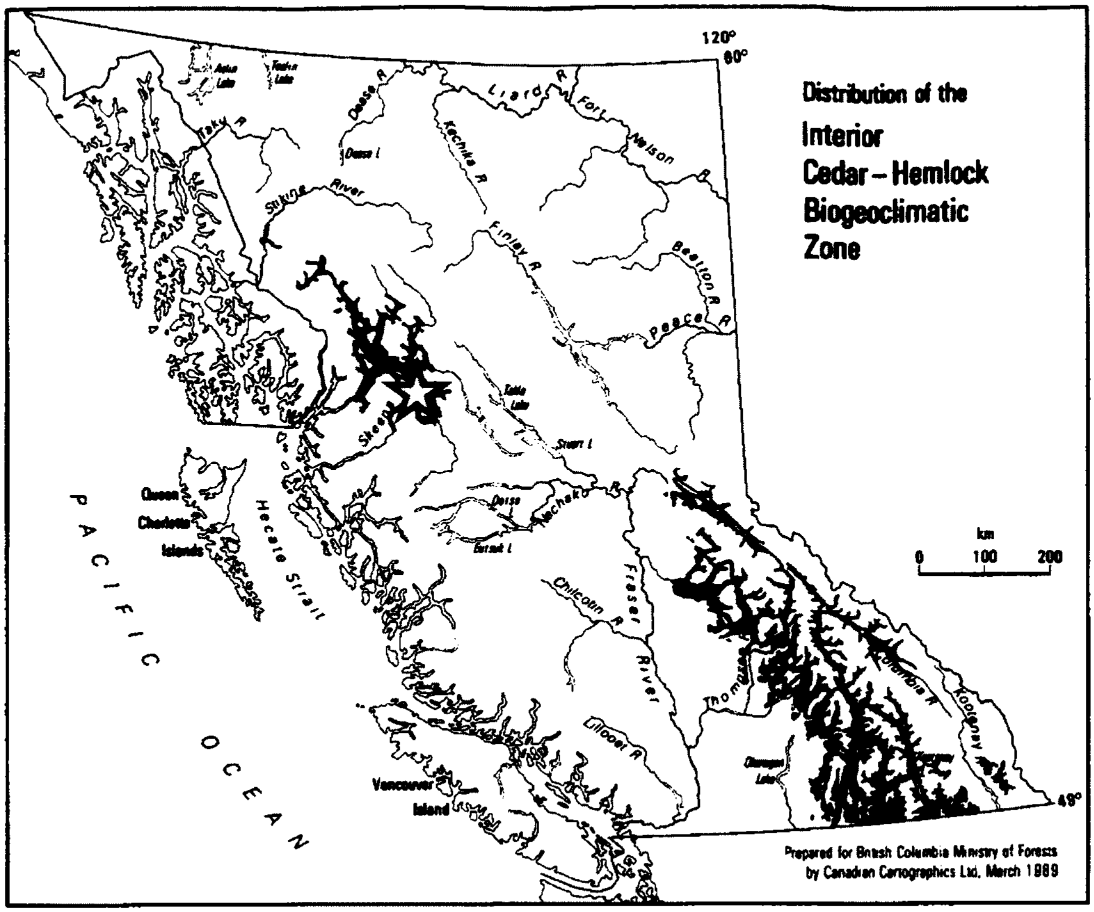

Figure 2: Distribution of the Interior Cedar-Hemlock Biogeoclimatic Zone in British Columbia. Figure from Meidinger and Pojar (1991). Grey star indicates location of research area.

The understory shrub layer consists of black huckleberry (*Vaccinium membranaceum*), devil's club (*Oplopanax horridus*) and some skunk cabbage (*Lysichiton americanus*). Characteristic herbaceous species are bunchberry, twinflower and queen's cup. The associated non-vascular species include red-stemmed associated non-vascular species include red-stemmed feathermoss, Knight's plume (*Ptilium crista-castrensis*) and step moss (*Hylocomium splendens*; Meidinger and Pojar 1991).

Study Sites

The study sites were located within 3 watersheds: 1) Ascaphus (AS); 2) Gosling (GO); and 3) Kleanza (KL; Figure 3). Sites within each of these watersheds were in the CWH zone and had portions that are old growth (i.e., age class 8 or 9; 141-250 years or > 250 years). Each of the sites was located adjacent to 3rd order (Strahler 1957) larval streams that are positioned in the middle or upper portions of 3rd order sub-basins (M. Todd Pers. Comm.).

I conducted my study across 3 sites representing forest retention treatments: 1) old-growth comprised of undisturbed stands >140 years; 2) stream-side forest retention (i.e., buffer) where harvesting has occurred at a distance of 30-50 m from the primary stream; and 3) clear-cut harvest of the site including the area adjacent to the stream edge. As harvesting began in 1987, one site had significant tree growth and was identified as representing forest regeneration (Table 1). All sites were located >50 meters from operational forest service roads.

History of harvest within the watersheds differed based on the time of road construction. For example, the Kleanza watershed was cut > 30 years and contained regenerating stands that were 25-30 years old. The Ascaphus watershed had 10-15 year old forest retention treatments, while the Gosling watershed was the most recent with harvesting occurring < 10 years in the past. Thus, the harvested stands ranged from age class 1 or 2 (0-40 years) and represented structural stages of 1 (immediately post disturbance) to 4 (pole saplings; BCMFR and BCMOE 2010).

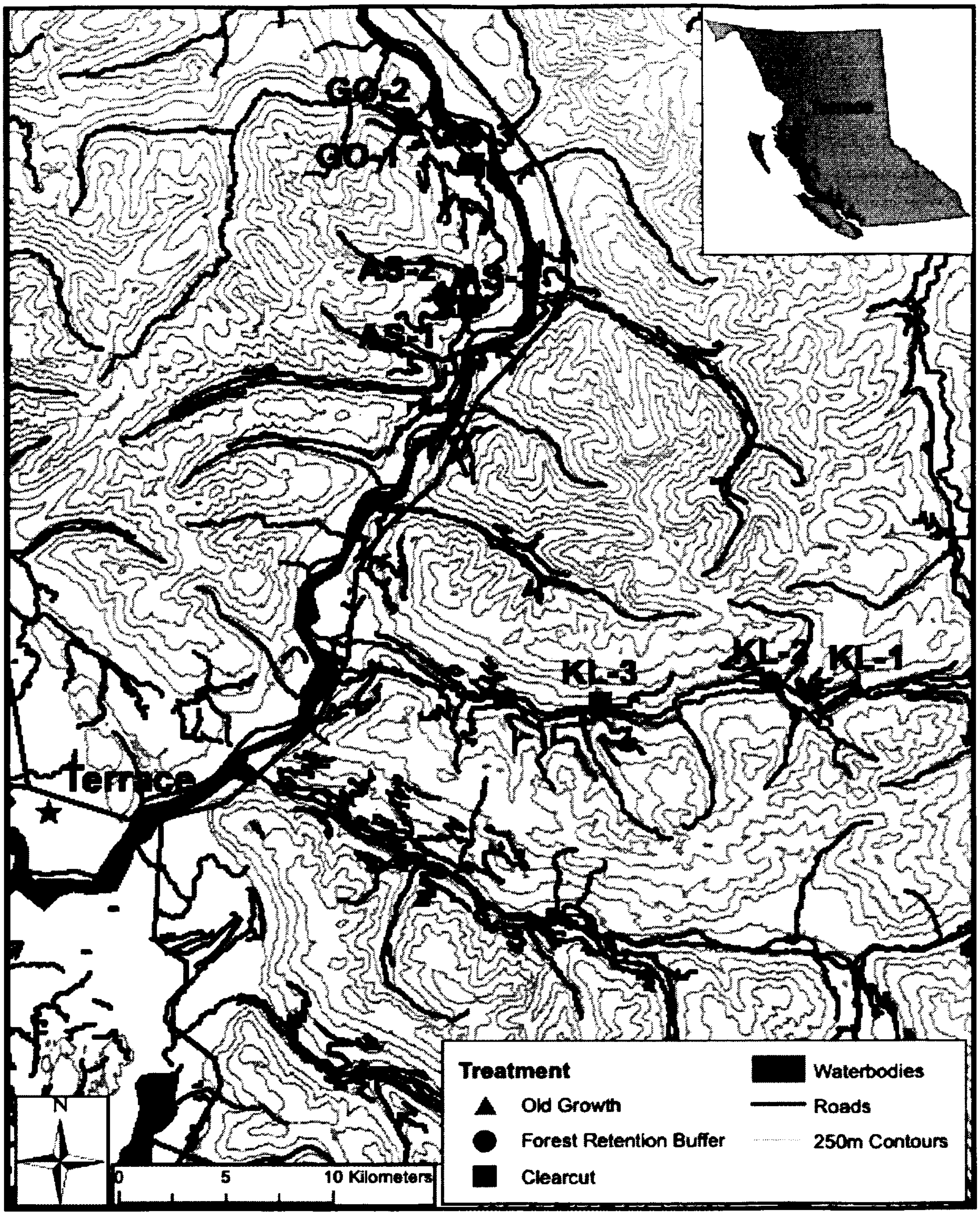

Figure 3: Location of the study watersheds, Gosling Creek (GO), Ascaphus Creek (AS) and Kleanza Creek, (KL) and treatments (1- old growth, 2- forest retention buffer and 3- clearcut) near Terrace, BC.

Table1: History of forest harvesting that has occurred within the watersheds for all forest retention treatments (old growth (OG), forest retention buffer (BF), regeneration (RG) and clearcut (CC)) east of Terrace, BC, where coastal tailed frog populations were monitored.

Watershed	**Forest Retention Treatment**	**Elevation (m)**	**Biogeoclimatic Ecosystem Classification**	**Dominant Canopy Condition**	**Dominant Understory**	**Harvest Date**	**Treatment Status**
Gosling	OG	463	CWHws1	>250 year old western hemlock and subalpine fir forest with multi-storied canopy.	Moist pockets of devil's club and skunk cabbage with *Vaccinium* species throughout.	N/A	Streamside OG. Opposite bank OG. Upstream OG.
Gosling	BF	417	CWHws1	>250 year old western hemlock and subalpine fir forest with a recently disturbed area outside of stream buffer.	Dominated by *Vaccinium* species, bracken fern (*Ptreidium aquilinum*), fireweed (*Chamerion angustifolium*), and logging debris with a few moist pockets of devil's club and skunk cabbage. Within the buffer only *Vaccinium* species.	2006	Streamside WHA core area reserve 30-50 m OG (average 40 m). Opposite bank OG. Upstream OG.
Gosling	CC	319	CWHws2	Western hemlock and subalpine fir found in streamside retention with dbh ≤ 30 cm. Recently disturbed site with no canopy outside of stream buffer.	Dominated by *Vaccinium* species with very few moist pockets of devil's club. Outside of buffer, dominate in fireweed and logging debris with very few moist pockets of devil's club and *Vaccinium* species.	1998 - 2010	Streamside variable width retention (average 30 m; range 0-50 m) with dbh ≤ 30 cm. Opposite bank CC with similar pattern of streamside retention Upstream CC with similar pattern of

							streamside retention.
Ascaphus	OG	550	CWHws1	141-250 year old western hemlock and subalpine fir forest, with western red cedar and Sitka spruce (*Picea sitchensis*) component. Multi-storied canopy.	Moist pockets of devil's club, skunk cabbage with *Vaccinium* species and false azalea) throughout.	N/A	Streamside OG. Opposite bank OG. Upstream OG immediately adjacent, with CC harvesting in headwaters.
Ascaphus	BF	582	CWHws1	141-250 year old western hemlock and subalpine fir forest, with western red cedar and Sitka spruce within streamside buffer. No dominant canopy outside of buffer.	*Vaccinium* species and a few moist pockets of devil's club within buffer. Dense *Vaccinium* spp and false azalea outside of buffer.	1994-1995	WHA core area reserve 40-50 m OG buffer. Opposite bank OG. Upstream OG immediately adjacent with CC harvesting in headwaters.
Ascaphus	CC	273	CWHws1	141-250 year old western hemlock and subalpine fir within streamside retention. Dense pole/sapling western hemlock and lodgepole pine (*Pinus cortata*) < 10 m tall outside of buffer.	*Vaccinium* species within streamside buffer with moist pockets of devil's club and red osier dogwood (*Cornus stolonifera*) by the stream.	1992-1995	Streamside variable width retention (average ≤ 25 m) with substantial blowdown. Opposite bank OG. Upstream OG immediately adjacent with CC harvesting in headwaters.
Kleanza	OG	801	CWHws2	> 250 year old western hemlock, amabilis and subalpine fir with	Few moist pockets of devil's club and skunk cabbage with *Vaccinium* species	N/A	Streamside OG. Opposite bank CC in 2009. Upstream OG.

				multi-storied canopy.			
Kleanza	BF	650	CWHws2	> 250 year old western hemlock, amabilis and subalpine fir. Multi-storied canopy within streamside buffer. Dense pole/sapling western hemlock and subalpine fir < 15 m tall outside of buffer.	*Vaccinium* species with some false azalea and moist pockets of abundant devil's club and skunk cabbage.	1977-1979	WHA core area reserve ~50 m OG buffer. Opposite bank CC (1991) and salvage logging (1997). Upstream OG.
Kleanza	RG	528	CWHws1	Dense pole/sapling western hemlock and subalpine fir < 20 m tall.	Poorly developed understorey with moist pockets of devil's club and lady fern.	1986-1987	Streamside no retention. Opposite bank CC in 1980. Upstream OG.

CHAPTER 2

FINE-SCALE DISTRIBUTION AND MOVEMENT PATTERNS OF POST-METAMORPHIC COASTAL TAILED FROGS

INTRODUCTION

The distribution and movement patterns of individual animals can reveal mechanisms that dictate the spatial ecology, population dynamics such as breeding phenology, and evolution of a species (Daugherty and Sheldon 1982). For example, many amphibians have biphasic life cycles requiring long-distance movements to and from breeding or over-wintering sites. During the summer, short excursions occur within relatively small patches of habitat related to specific climactic conditions and food (Semlitsch 2008). To understand how such movements relate to broader population processes, one must conduct studies that reveal the interactions between the environment and the species' spatial ecology. Such inferences have both theoretical and applied applications, especially for amphibian species influenced by human development and habitat alteration (Semlitsch 2008).

Ascaphus truei, coastal tailed frog, is endemic to the Pacific Northwest. They are habitat specialists with life-history requirements closely associated with forests of this region. The tailed frog can live between 15-20 years and depending on the geographical location, take 1-5 years to metamorphose (Daugherty and Sheldon 1982). Water temperatures > 18.5°C can affect embryonic development of larvae and adults are susceptible to ambient air temperatures > 24°C (Claussen 1973b; Brown 1975). This species is also less tolerant to desiccation than other amphibians and requires forest stands with a complex understory (Claussen 1973a, 1973b; Daughtery and Sheldon 1982).

The response of tailed frog larvae to forest practices has been relatively well documented because of the ease of working with this life stage (Corn and Bury 1991; Wallace and Diller 1998; Wahbe and Bunnell 2001). Conversely, tailed frogs inhabiting terrestrial habitats are difficult to locate because of cryptic colouring, relatively small size, movement through or occupancy of downed and rotten wood and nocturnal activity patterns (Metter 1967; Green and Campbell 1984). The removal of overstory and reduction in structural complexity in the understory can restrict the distribution of post-metamorphic tailed frogs with implications for survival and reproduction (Hawkes and Gregory 2012).

When occupying unmodified habitats, adult tailed frogs are extremely philopatric to the larval stream (Wahbe *et al.* 2004; Matsuda and Richardson 2005; Burkholder and Diller 2007). Reproductive females of southerly populations have been observed to alter their distribution depending on the time of year such as moving upstream after ovipositioning or downstream to breed (Landreth and Ferguson 1967; Brown 1975; Wahbe *et al.* 2004; Hayes *et al.* 2006). Burkholder and Diller (2007) also concluded that females moved greater longitudinal distances along the stream edge in comparison to adult males and juveniles.

Previous research on southerly populations of the tailed frog has demonstrated variation in the spatial distribution of age classes (adult versus juveniles). Wahbe *et al.* (2000) found that reproductive adults were more common along the stream edge and suggested that this was reflective of philopatry. Additionally, Wahbe *et al.* (2000) captured the majority of newly metamorphosed tailed frogs 100 m from the stream edge suggesting dispersal by younger animals. Alternatively, Burkholder and Diller (2007) noted that both immature and adult tailed frogs exhibited site fidelity. Conversely, Matsuda and Richardson (2005) demonstrated no significant age- or habitat-specific differences in the direction of movement, but found a greater proportion of individuals moved parallel with the stream.

Within BC, the alteration and loss of terrestrial habitat for tailed frogs can be attributed to clear-cut logging and associated road construction (Deguise and Richardson 2009). Removal of overstory changes the light, temperature, humidity, and soil moisture within a stand. For example, once the overstory canopy is removed an increase in the amount of light penetrating the understory increases the temperature and decreases the soil moisture (Brofoske *et al.* 1995). Because amphibians may undergo long-distance movements for dispersal and demonstrate fidelity to breeding sites, a change in the environment can create barriers that affect population connectivity at multiple spatial scales (deMaynadier and Hunter 1995; Gibbs 1998; Knapp *et al.* 2003; Wahbe *et al.* 2004; Hawkes and Gregory 2012). Understanding the processes that influence site fidelity and associated movements not only provides insights into the ecology of tailed frogs, but also increases our understanding of how habitat change influences the dynamics of individual populations (Daugherty and Sheldon 1982).

CHAPTER PREDICTIONS

Drawing on the existing literature, I tested 3 predictions that described and explained the fine-scale distribution and movement of the tailed frog at their northern extent in western BC. I used systematic pitfall data to summarise capture rates by demographic, temporal, environmental and treatment variables suspected to influence relative abundance and fine-scale distribution. I monitored the movement of frogs across 4 forest retention treatments: 1) recent clearcut with variable stream retention; 2) clearcut with regeneration (< 25 year post harvest); 3) forest retention at the larval stream (Wildlife Habitat Area 50-m core reserve); and 4) forest retention across the study site.

Demographics and movement – I predicted that the gender and age of a tailed frog would influence movement and distribution. Juveniles would be located at greater distances from the stream edge in all 4 treatments; this pattern of distribution reflects dispersal behavior observed in other studies. Furthermore, I predicted that the movement patterns of reproductive-aged tailed frogs would correspond with the ovipositioning and breeding periods.

Forest retention treatment and movement – I predicted that tailed frogs in old-growth habitats would be captured at greater distances from the stream edge relative to habitats with forest harvesting. This pattern of movement was in response to environmental constraints resulting from reduced forest complexity and microclimatic conditions that exceeded the physical tolerance for dry and warm environments.

Weather and movement – I predicted that tailed frogs would demonstrate more active and dynamic movements and be located further from the stream edge when weather conditions (i.e., rainfall events, temperature and relative humidity) were more suitable for above-ground terrestrial movements.

METHODS

Study Area

The study area was situated on the leeward side of the Coastal Mountains in northwestern British Columbia. Vegetation communities included the Coastal Western Hemlock (CWH) and some transitional species associated with the Interior Cedar-Hemlock (ICH) Biogeoclimatic Ecosystem Classification (BEC) zones. The CWH has mild temperatures and heavy rainfall with climax forests of western hemlock (*Tsuga heterophylla*) and amabilis fir (*Abies amabilis*). The ICH, reflective of a transitional climate between coastal and interior stands, contained climax forests of western hemlock and subalpine fir (*Abies lasiocarpa*). The main disturbance across these study sites was timber harvest. See Chapter 1 for a more detailed description of the study area.

Pitfall data were collected during 2012 and 2013 from sites in the Gosling (GO) and Kleanza (KL) watersheds. Sites in each watershed were classified as 1 of 4 categories representing forest harvest history within the watershed: 1) no history of harvest; 2) a forest retention buffer (30-50 m) 3) clearcut with minimal (dbh ≤ 30 cm) to no overstory canopy; and 4) regeneration (< 25-year overstory).

The GO sites were located within the transition zones between the CWHws and the ICHmc2 (Meidinger and Pojar 1991). Study sites were classified as CWHws1 or CWHws2 and situated at relatively low elevations (319-463 m above sea level (asl)). These sites were dominated by clearcut or old (> 250 years) western hemlock and amabilis fir with moist pockets of devil's club (*Oplopanax horridus*), skunk cabbage (*Lysichiton americanus*) and abundant *Vaccinium* species. Most harvesting in this watershed occurred recently (< 5 years) resulting in no tree canopy and substantial growth of fireweed (*Chamerion angustifolium*) and bracken fern (*Pteridium aquilinum*) where logging had occurred.

The sites within the KL watershed were also found within two variants of the Coastal Western Hemlock BEC zone (CWHws2, CWHws1). Two sites were located at higher elevations (650 m and 801 m asl; CWHws2). The old growth treatment had > 250 year old western hemlock, amabilis and subalpine fir in a multi-storied canopy; while the forest retention buffer treatment contained 50 m of > 250 year old western hemlock, amabilis and subalpine fir along the stream. Both contained moist microsites in the understory with abundant devil's club and skunk cabbage. The third site was lower in elevation (528 m asl; CWHws1) and had dense pole/sampling regeneration of western hemlock and lodgepole pine (*Pinus contorta*) < 20 m tall. This site was harvested in 1987 and had poorly developed understory with moist pockets of devil's club and lady fern (*Athyrium filix-femina*).

Data Collection

I installed 288 pitfall traps within the 2 watersheds (n = 144 per watershed). Each trap was 38 cm in depth and 15 cm in diameter. A plastic insert was put in place to limit escape of tailed frogs by jumping. To limit rodent mortality, a length of 40-cm twine was secured to the insert (Karracker 2001); however, after the 2012 trap session, the twine was knotted to better allow escape by rodents (Appendix I).

Within each watershed we installed 36 pitfall arrays each containing 4 traps and 2 perpendicular arms of 10-m lengths of drift fencing (Matsuda 2001). Arrays were placed systematically at 4 distances (5, 30, 55 and 80 m) from the known larval stream for a total of 3 arrays (12 traps) at each distance (Figure 4A). Each captured tailed frog was assigned a direction of movement according to the drift fence orientation relative to the adjacent stream. Tailed frogs were recorded as moving downstream (with the flow of water), upstream (against the flow of water), away from the stream, and toward the stream (Figure 4B).

Trap session duration – To control for temporal influences on tailed frog behavior, all traps within a watershed were open simultaneously and were visited daily during the months of June-October for a 6-night period. During 2012, 3 trap sessions were conducted from mid-July until the end of October resulting in 5,184 trap nights. For 2013, 3 trap sessions were run across 5 months (June-October) resulting in 6,192 trap nights (Table 2).

Tailed frog morphometrics- For each captured tailed frog I recorded the snout vent length (SVL), shank length (SL), weight and gender (male or female) based on visible sexual characteristics (external cloaca, breeding pads or eggs present). I classified each animal as adult (reproductive); juvenile (pre-reproductive) or metamorph (containing rudimentary tail). The reproductive status of adults was determined by the visibility of eggs in females (gravid) or darkened breeding pads in males (breeding). I used visual implant elastomer (VIE; Northwest Marine Technologies, Inc.) to permanently mark each individual with a unique colour combination. If a tailed frog was < 2.0 g a mark indicating only year and watershed was assigned.

Statistical Methods

Data analysis

Presence of tailed frogs within a trap allowed me to quantify the activity of each demographic and age class relative to forest retention treatment, distance from stream, season, weather and microclimate data. I applied statistical count models relating the number of tailed frogs captured per day in each trap to temporal, site, and environmental variables. Count models accommodate both over dispersion and presence of excess zeros (i.e., traps with no counts), a common occurrence in ecological data (Nielsen *et al.* 2005). Following extensive testing, I determined that the distribution of count data was too infrequent for a Poisson or negative binomial distribution. Thus, I compressed the count data to a binary variable (0 = no catch, 1= ≥ 1 catch) and used logistic regression to calculate the likelihood of capturing a tailed frog in a trap. Combinations of variables within each logistic regression model served as hypotheses representing ecologically plausible explanations for the capture of at least one tailed frog (Appendix II and III; Table 3). The number of tailed frogs captured was not sufficient (n = 129 in 2012 and n = 31 in 2013) to split model sets into adult (reproductive) and juvenile (pre-reproductive) age classes. However, to control for a difference in years, I tested identical model sets for both 2012 and 2013.

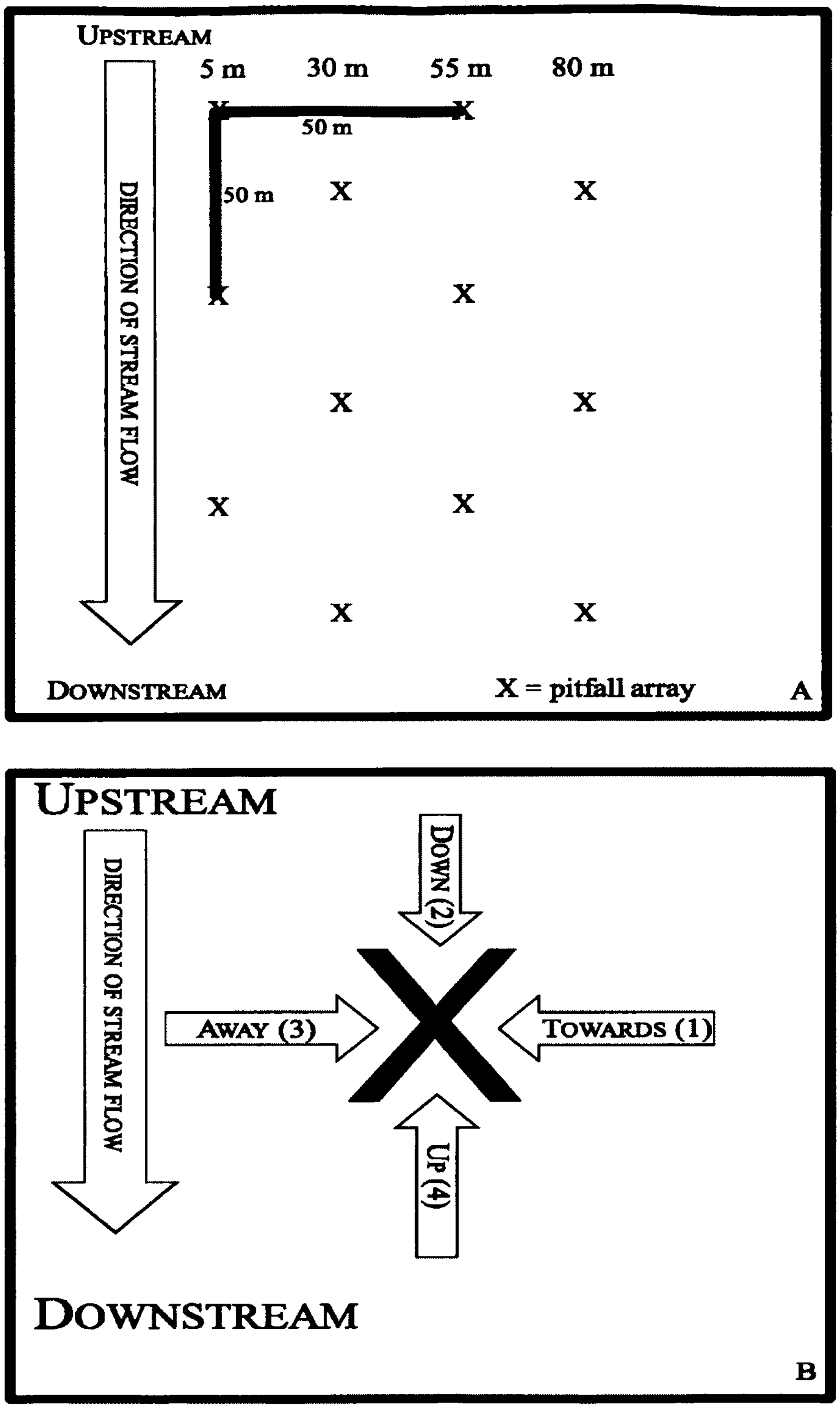

Figure 4: Trap arrays for tailed frogs applied to 3 forest retention treatments found within two watersheds (A). Each array (X) contained 4 traps centered in 2 perpendicular arms of 10m of drift fencing for a total of 288 traps. Each trap within the array was used to monitor direction of tailed frog movement in relation to the known larval stream, towards (1), down (2), away (3) and up (4) stream (B).

Table 2: Trap session dates and observed seasonal life cycle of the tailed frog for 2 watersheds east of Terrace, BC, surveyed during 2012 and 2013.

Year	Watershed	Dates	Session	Life cycle
2012	Gosling	July 17-22	Spring	ovipositioning
	Kleanza	July 22-27	Spring	ovipositioning
	Gosling	August 25-30	Summer	foraging
	Kleanza	August 19-24	Summer	foraging
	Gosling	October 9-14	Fall	breeding
	Kleanza	October 1-6	Fall	breeding
2013				
	Kleanza	June 2-8	Spring	ovipositioning
	Gosling	July 3-8	Spring	ovipositioning
	Kleanza	August 7-12	Summer	foraging
	Gosling	August 16-21	Summer	foraging
	Kleanza	September 10-16	Fall	movement to breeding sites
	Gosling	September 27-October 2	Fall	movement to breeding sites
	Gosling	October 3-8	Fall	movement to breeding sites/breeding

I used variance inflation factors (VIF) to assess multicollinearity among covariates. An individual VIF > 10 or a mean VIF > 1 suggested that a model had high levels of multicollinearity (Chatterjee *et al.* 2000).

Temporal variable – Trapping sessions were assigned a categorical variable to distinguish the month. During 2012, sessions occurred on: 1) July 17th-27th; 2) August 19th-30th; and 3) October 1st-14th. In 2013, the number of sessions and temporal dispersion of effort increased: 1) June 2nd-8th; 2) July 3rd-8th; 3) August 7th-12th and 16th-21st; 4) September 11th-16th and September 27th- October 2nd; and 5) October 3rd-8th (Table 2).

Site variables – For each pitfall array, I measured habitat variables at a 25-m^2 plot (2.82-m radius). I measured the percent coverage of shrubs and trees < 2 m (B_1) and those > 2 m, but < 10 m (B_2; Ministry of Forests 1998). These layers were used in combination with indicator plants to quantify the site moisture at each trap array.

Sites in each watershed were classified as 1 of 4 canopy covers based on the forest harvest history within the watershed: 1) no history of harvest (n = 96 traps); 2) a forest retention buffer (30-50 m; n = 96) containing trees > 250 years old and a distinct edge from a previous cut; 3) clearcut with minimal (dbh ≤ 30 cm) to no overstory canopy (n = 48); and 4) regeneration (< 25-year overstory; n = 48). This variable represented the overstory and structural complexity at each site. Trap numbers varied among disturbance categories.

Each trap array was classified into 1 of 3 categories according to the distance of the array from the clearcut (hard) edge: 1) located between the stream edge and > 10 m from the clearcut edge; 2) ≤ 10 m on either side of the hard edge; and 3) > 10 meters from the hard edge within a clearcut. Additionally, I used a spherical densiometer to quantify the percent canopy closure.

I used the Ecosystems of BC (Meidinger and Pojar 1991) for the Prince Rupert Forest Region and indicator plant species within the 25-m^2 plot, to quantify site moisture as: 1) 'dry' if no species associated with wet ecosystems were present; 2) 'mesic' when devil's club was < 10% with minimal oak fern (*Gymnocarpium dryopteris*); 3) 'subhygric' when < 20% devil's club was present and dominant in oak fern; and 4) 'hygric' when the site had > 20% devil's club and was dominated by lady fern or trees with affinity for wet soil (e.g., *Salix* spp.).

Within the 2 watersheds, site elevations ranged between 325-801 m asl. I used a Gaussian term to account for the nonlinear influence of site elevation on the distribution of tailed frogs. This equation consisted of both the linear component, which identified the increase in tailed frog captures, and a squared component to identify at what elevation tailed frog presence decreased as a function of increasing elevation.

Environmental variables – For each trap day I used microclimate stations and field observations to measure weather: air temperature, relative humidity, and days since last rain. Microclimate stations were deployed at 5, 30, 50, 100 m from the stream edge and consisted of 1 DS1923-F5 Hygrochron (temperature and relative humidity) iButton data logger (Maxim Integrated) suspended 1 m above the ground under a radiation shield (M. Todd Unpub. Data). From those data I calculated the maximum and minimum temperature and humidity in a 24-hour period (10 a.m.–10 a.m.) as well as the difference between the maximum and minimum. Similar to elevation, the temperature variable was fit as a nonlinear Gaussian function.

Table 3: Independent variables used to model the occurrence and abundance of tailed frogs captured in pitfall traps in 2 watersheds east of Terrace, BC, during 2012 and 2013.

Theme	**Variable**	**Variable Description**
Temporal	year	Year of trap sessions: 1) 2012 and 2) 2013
	trap month	Trap month. 2012: 1) July; 2) August; and 3) October. 2013: 1) June; 2) July; 3) August; 4) September; and 5) October.
Treatment	canopy cover	Overstory tree coverage: 1) old growth; 2) harvested buffer; 3) clearcut; 4) regeneration.
	densiometer	Percent canopy opening at the pitfall array.
	site moisture	Inferred site wetness based on BEC indicator plants in the 25-m^2 plot: 1) zonal series (dry); 2) mesic; 3) subhygric; and 4) hygric (page 29).
	distance to edge	Distance of trap arrays from hard edge: 1) stream edge to < 10 m from hard edge; 2) arrays ± 10 m of the hard edge; and 3) arrays > 10 m from a hard edge.
	distance to stream	Straight-line distance from the larval stream edge.
	orientation	Trap arrangement within array indicating direction of tailed frog movement in relation to larval stream: 1) towards; 2) down; 3) away; and 4) up.
	site elevation*	Elevation in meters defining the start point of a site in the forest retention treatment.
Environment	temp$_{MAX}$*	Maximum temperature over a 24-hour period using two-microclimate transects.
	temp$_{MIN}$*	Minimum temperature over a 24-hour period using two-microclimate transects.
	temp$_{varibility}$	Difference between the maximum and minimum temperatures over a 24-hour period.
	humidity$_{MAX}$	Maximum humidity over a 24-hour period using two-microclimate transects.
	humidity$_{MIN}$	Minimum humidity over a 24-hour period using two-microclimate transects.
	humidity$_{varibility}$	Difference between the maximum and minimum humidity over a 24-hour period.
	days since last rain	Number of days since the last precipitation event.

*Variable had Gaussian term applied to represent a non-linear relationship.

Model selection

I used Akaike's Information Criterion for small samples (AIC_c) to rank and select the most parsimonious logistic regression model. I used ΔAIC_c to identify the 'best' model of the set and Akaike weights ($AICw$) to quantify model selection uncertainty. If models were nearly equivalent (i.e., $\Delta AIC_c < 2$), then I selected the model with the fewest number of parameters (Johnson *et al.* 2006).

I used AIC_c to test whether repeated sampling within a treatment, trap array or trap warranted a mixed effects model (i.e., random effect for multiple sampling within fixed treatment). I determined that a full mixed effect model was not warranted. However, I used the cluster option within Stata (ver.12.1, StataCorp LP, 2012) to correct the variance for repeated sampling at a trap (Williams 2000; Nielson *et al.* 2001).

Model and variable evaluation

I calculated the Area Under the Curve (AUC) for the Receiver Operating Characteristic (ROC) to test the predictive performance of the most parsimonious model. The curve evaluates the proportion of correctly and incorrectly classified predictions over a continuous range of probability thresholds from 0 to 1.0 (Pearce and Ferrier 2000). Scores of 0.5-0.7 suggest a poor model, 0.7-0.9 a good model, and 0.9-1.0 a highly predictive model (Swets 1988). When performing the ROC test I withheld each trap record sequentially from the model building process and then used that withheld record to generate a predicted probability. Thus, a bootstrapping-like process resulted in an independent evaluation of the predictive performance of the logistic regression model.

I used 95% confidence intervals to assess the relative strength of the coefficients within the most parsimonious model. When intervals do not overlap zero, covariates are considered as a significant factor influencing the distribution of tailed frogs. All statistical analysis was conducted using Stata (ver.12.1, StataCorp LP, 2012).

RESULTS

Capture statistics

In 2012, 5,184 trap nights resulted in the capture of 129 tailed frogs (63 female, 29 male, 37 juveniles or metamorphs) for a catch per unit effort (CPUE) rate of 2.49 tailed frogs/100 trap nights. An increased trap effort in 2013 resulted in 6,192 trap nights and the capture of 31 tailed frogs (14 female, 14 male, 3 juveniles) with 0.50 tailed frogs/100 trap nights. Over the 2 years, adults in the old growth had the greatest CPUE with 1.30 individuals/100 trap nights (Table 4). Juveniles had the greatest CPUE in the regeneration treatment (0.45 individuals/100 trap nights) and metamorphs in the clearcut (0.55 individuals/100 trap nights). In both years, 95% confidence intervals revealed that females had a significantly greater average weight (wt), snout-vent length (SVL) and shank length (SL) when compared to males (Figure 5).

Variation in microclimate

During 2012, the GO watershed had more rain events closer together in the summer and fall compared to the spring. In the KL watershed more rain events occurred during the summer trapping session compared to the fall or summer (Appendix IV). In 2013, the fall trapping sessions had far more rain events in the GO compared the KL watershed (Appendix V).

Table 4: Total number of tailed frogs captured and the catch per unit effort (CPUE) for each age class and 4 forest retention treatments (old growth, forest retention buffer, regeneration, and clearcut) for 2 watersheds located east of Terrace, BC, during 2012 and 2013. CPUE represents the number of individuals/100 trap nights.

Forest retention treatment	**Number of trap nights**	**Adults**	**CPUE**	**Juveniles**	**CPUE**	**Metamorphs**	**CPUE**
Both years							
Old growth	3792	48	1.30	7	0.18	4	0.11
Forest retention buffer	3792	38	1.00	11	0.32	4	0.11
Regeneration	1776	18	1.00	8	0.45	0	0
Clearcut	2016	7	0.35	4	0.20	11	0.55
2012							
Old growth	1728	43	2.49	5	2.89	4	0.23
Forest retention buffer	1728	24	1.39	12	0.69	4	0.23
Regeneration	864	11	1.27	8	0.93	0	0
Clearcut	864	6	0.69	2	0.23	11	1.27
2013							
Old growth	2064	5	0.24	2	0	0	0
Forest retention buffer	2064	14	0.68	0	0	0	0
Regeneration	912	7	0.77	0	0	0	0
Clearcut	1152	1	0	2	0.17	0	0

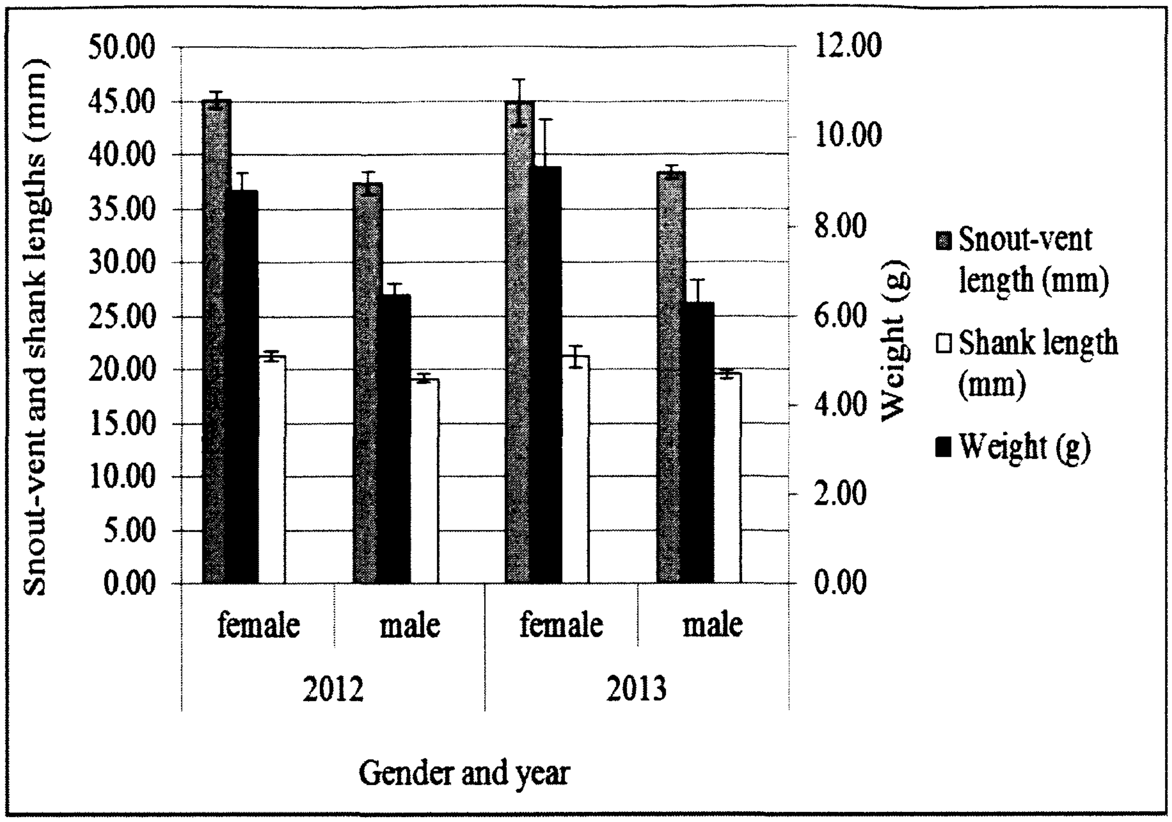

Figure 5: Weight (grams), snout-vent-length (mm) and shank lengths (mm) including 95% confidence intervals of adult tailed frogs in 2 watersheds located east of Terrace, BC, during 2012 and 2013.

Mircoclimate arrays in each watershed during 2012 demonstrated that temperatures for the 5-m arrays were comparable to the respective 80-m arrays for the old growth and clearcut treatments. However, the 5-m temperature arrays in the forest retention buffer treatments were similar to the old growth, while the 80-m arrays were more reflective of arrays at the same distance located in the clearcut or regeneration treatments (Figure 6). Additionally, microclimate arrays in 2013 demonstrated greater variability in weather patterns compared to those observed in 2012 (Figure 7).

Orientation of movement

The greatest proportion of tailed frogs captured in this study were found moving perpendicular (away or towards; 69.4%) to the stream rather than parallel (upstream or downstream; 30.6%). The orientation of movement was largely influenced by adults for 3 of the treatments (old growth, forest retention buffer, and regeneration). For example, in the old growth, tailed frogs had the greatest proportion of captures moving away from the stream (59%; Figure 8); however, this was largely attributed to post-ovipositioning females. Conversely, tailed frogs within the clearcut were evenly distributed between perpendicular and parallel movement. Fewer adults were present in these treatments which resulted in metamorphs influencing the observed orientation of movement (50% of captures) (Figure 8).

Distance of capture from stream

Of the 160 individuals captured, 56.9% were located in the 5-m trap arrays (n = 80 in 2012 and n = 11 in 2013). As the distance from stream increased, the number of individuals captured decreased with a total of 44 tailed frogs captured in arrays ≥ 55 m (Figure 9). Across all treatments, adults were most likely captured in arrays ≤ 30 m from the larval stream (59.5% of adult captures).

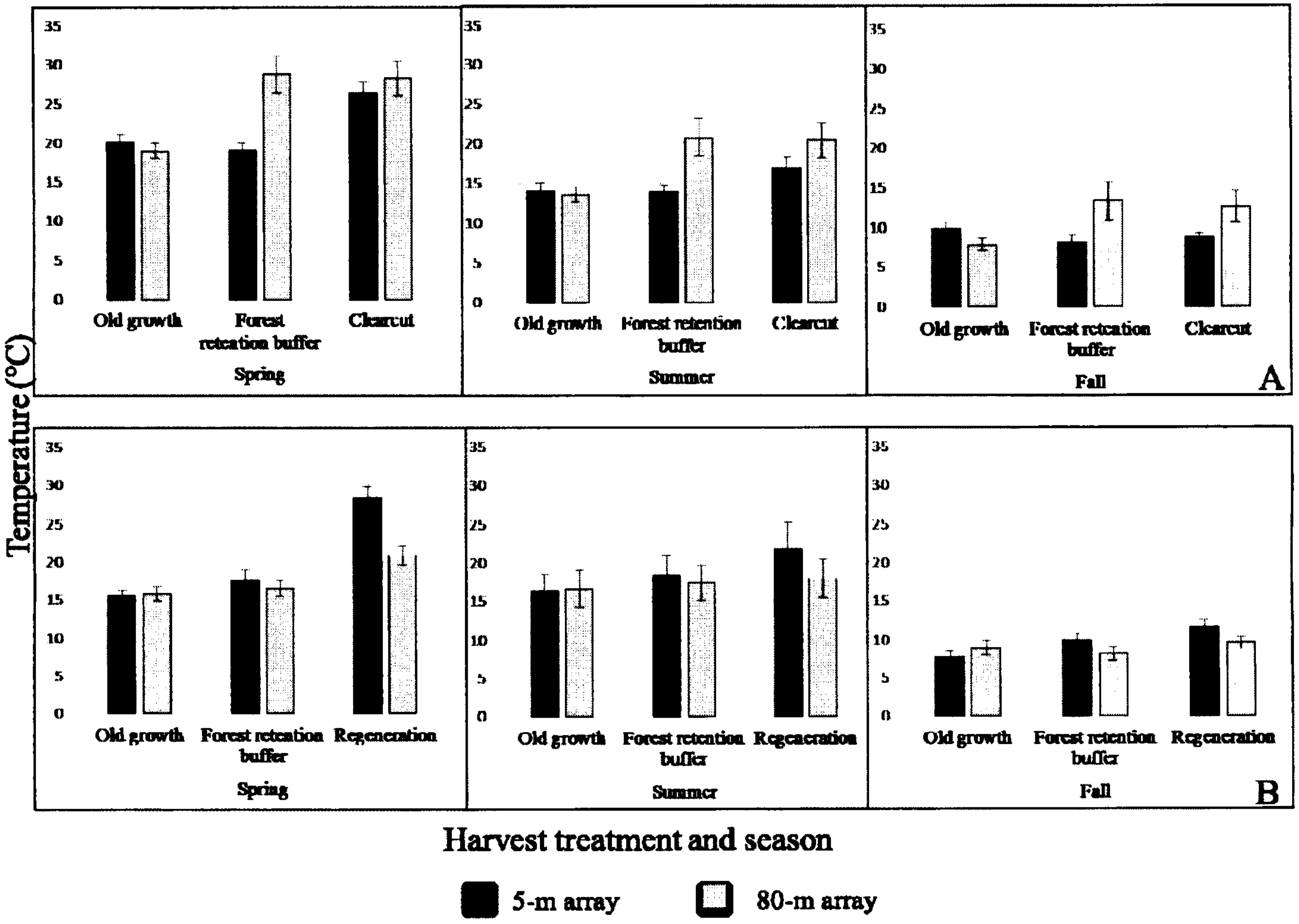

Figure 6: Microclimate arrays demonstrating the temperature variations between 4 forest retention treatments (old growth, forest retention buffer, regeneration and clearcut) located in the Gosling (A) and Kleanza (B) watershed, east of Terrace, BC, during 2012.

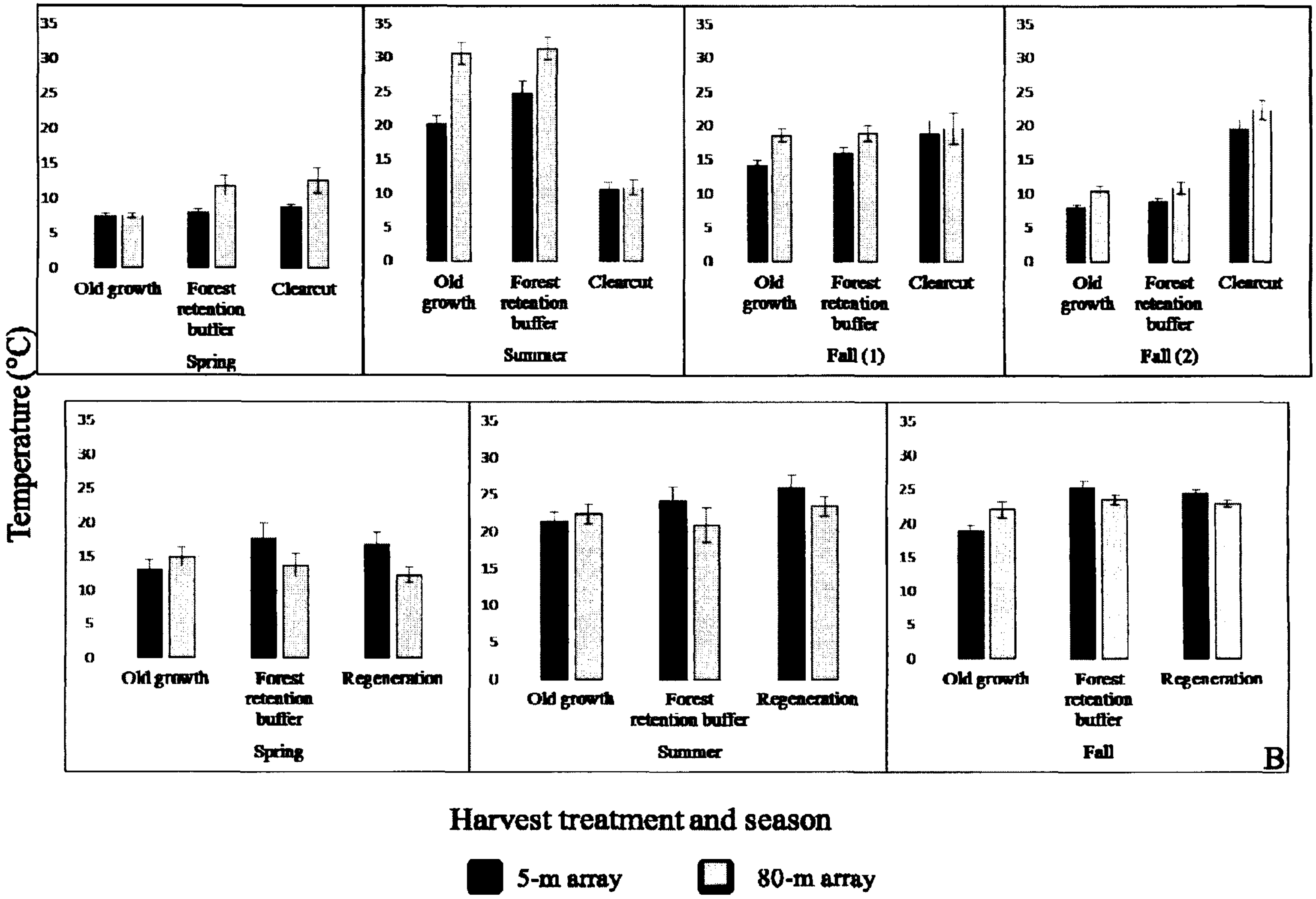

Figure 7: Microclimate arrays demonstrating the temperature variations between 4 forest retention treatments (old growth, forest retention buffer, regeneration and clearcut) located in the Gosling (A) and Kleanza (B) watershed, east of Terrace, BC, during 2013.

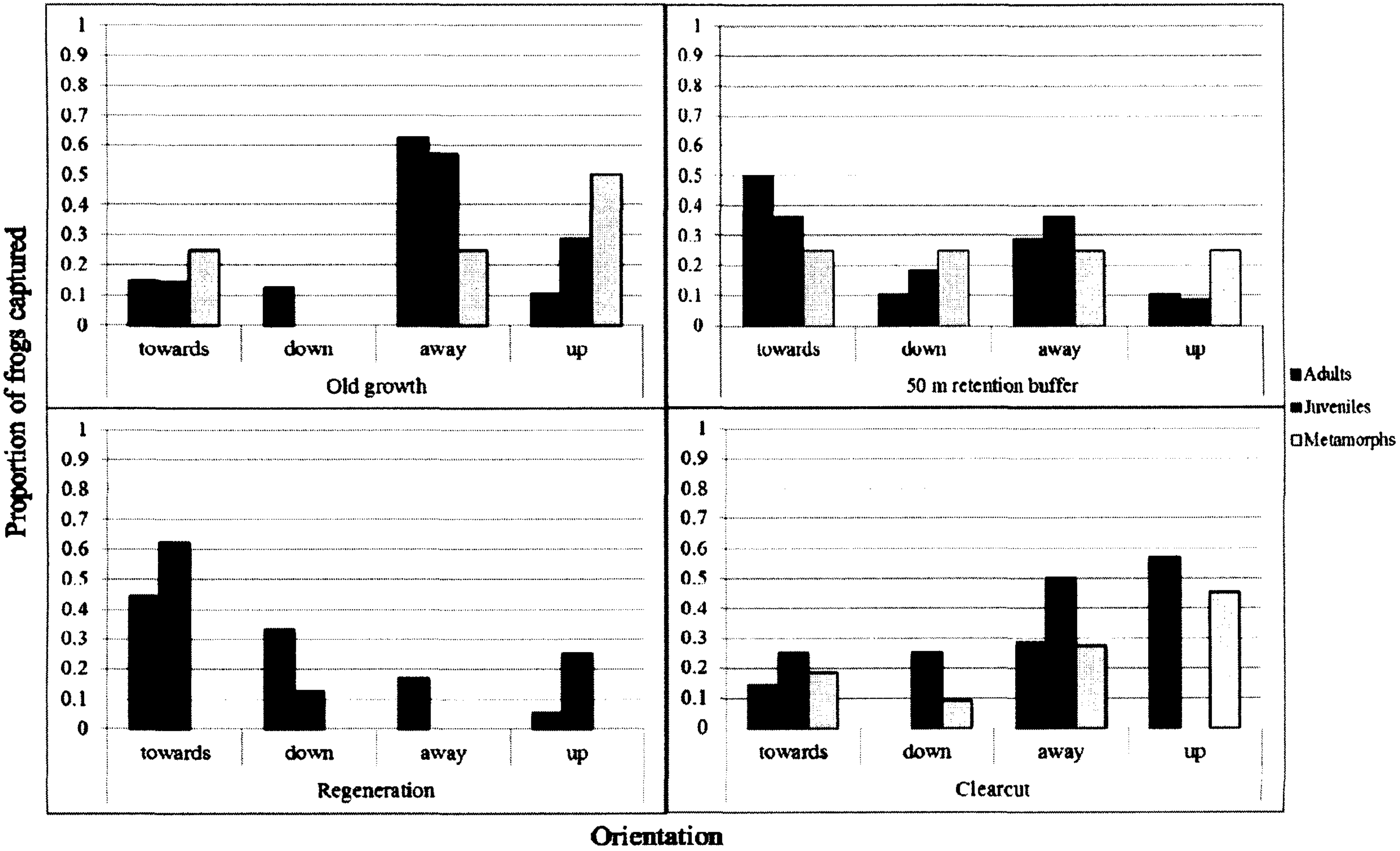

Figure 8: Proportions of tailed frogs captured for each age class relative to the direction of movement within each forest retention treatment (old growth, forest retention buffer, regeneration, and clearcut) for two watersheds located east of Terrace, BC, during 2012 and 2013. In the old growth a total of 59 tailed frogs were captured (48 adults, 7 juveniles and 4 metamorphs). The forest retention buffer had 53 tailed frogs (38 adults, 11 juveniles and 4 metamorphs), the regeneration treatment had 26 tailed frogs captured (18 adults, and 8 juveniles), and the clearcut had 22 individuals captured (7 adults, 4 juveniles and 11 metamorphs).

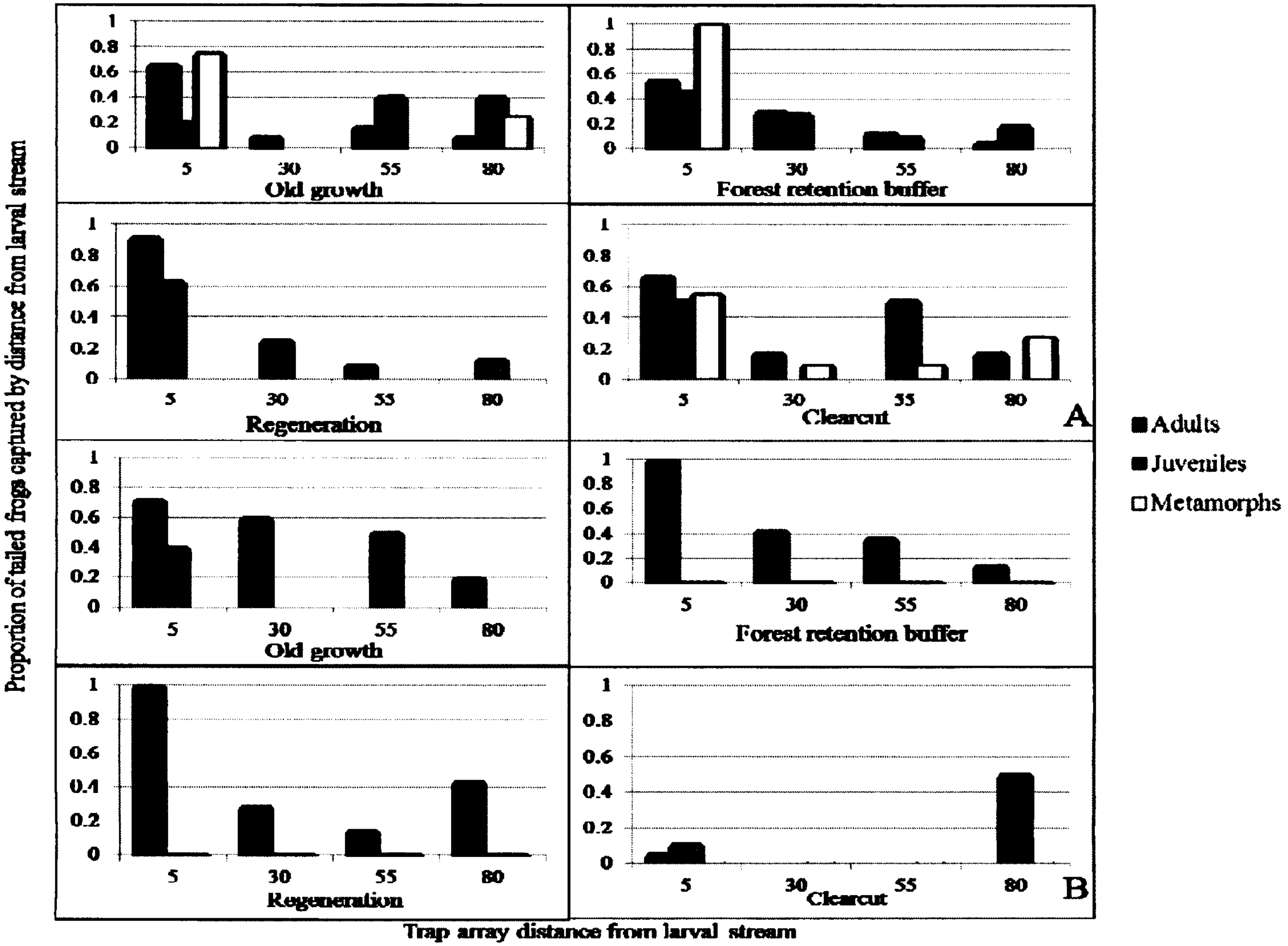

Figure 9: Proportions of tailed frogs captured within each forest retention treatment by age class and the distance from stream of trap array for 2 watersheds east of Terrace, BC during 2012 (A) and 2013 (B). In 2012, 52 tailed frogs captured in the old growth, 39 individuals in the forest retention buffer, 19 individuals in the regeneration treatment and 19 individuals in the clearcut.

Juveniles and metamorphs were captured primarily in the 5-m arrays (40% and 68%, respectively) when captures from forest retention treatments were pooled. However, within the old growth and clearcut treatments, juveniles had > 70% of their captures in arrays > 55 m from the larval stream (71.5% in old growth and 75% in clearcut). Conversely, juveniles in the forest retention buffer and regeneration treatments had < 30% of captures in arrays > 55 m from the larval stream (27.3% 50-m forest retention and 12.5% in regeneration).

Forest retention treatment

Of the 160 tailed frogs captured over the 2 years, 59 individuals were captured in the old growth (n = 2 sites), 53 were located in the forest retention buffer treatments (n = 2), 26 were found in the regeneration treatment (n = 1), and 22 were found in the clearcut treatment (n = 1; Table 2). However, capture rates for the three age classes of tailed frogs differed among forest retention treatments. The greatest CPUE for adults was in the old growth treatments (1.3 adults/100 trap nights) with more juveniles (0.45 individuals/100 nights) and metamorphs (0.55 individuals/100 trap nights; Table 2) being captured in the regeneration and clearcut treatments, respectively. Additionally, the number of tailed frogs captured in each of the forest retention treatments varied across the two years of sampling. In 2012, the greatest proportion of captures was in the old growth treatments (3.0 tailed frogs/100 trap nights) whereas in 2013 the greatest capture rates was in the regeneration treatment (0.77 tailed frogs/100 trap nights).

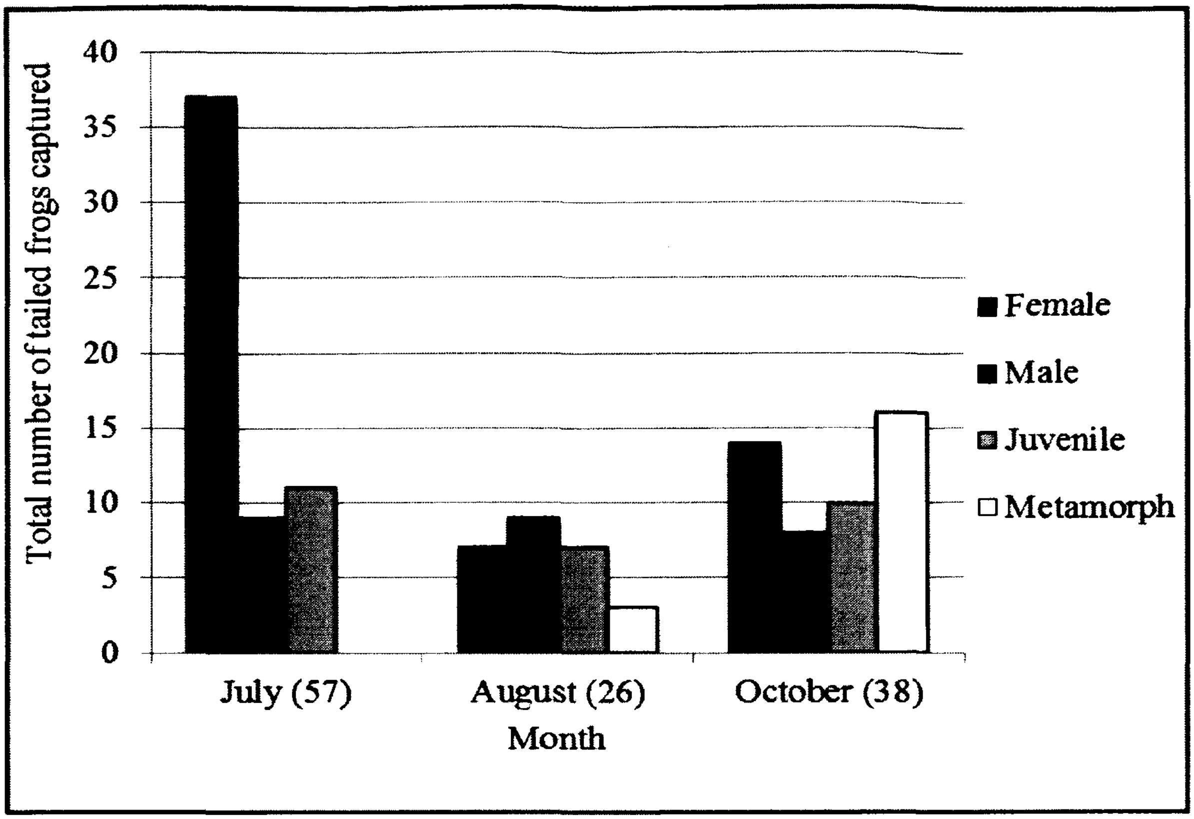

Figure 10: Total number of reproductive and pre-reproductive tailed frogs captured by month during 2012 in 2 watersheds located east of Terrace, BC. Numbers in brackets represent total captures within a month.

Temporal pattern of movement

Adult tailed frogs demonstrated differences in the rate of capture depending on the time of year and gender (Figure 10). For example, females were found in traps during months associated with the species' breeding phenology (i.e., spring and fall) and were distributed closest to the stream at this time. During July, females were either gravid or showed indications of post-ovipositioning while in October captured tailed frogs displayed breeding characteristics such as darkened breeding pads in males and visible eggs in females. Consistent with the known chronology of larval development, metamorphs began to emerge in August, as the oldest larvae metamorphose with their greatest occurrence in traps during October (Figure 10).

Statistical models

There was little model selection uncertainty for the 2012 capture year as two logistic regression models were responsible for the majority of the AIC_c weight (Table 5). The highest ranked model contained temporal, treatment, and environmental variables. However, the second highest ranked model (distance to stream + trap month + site elevation2 + days since last rain) was only slightly more parsimonious ($k = 8$) and therefore selected as the 'best' model of the set. The ROC test based on independent data suggested that 'good' predictive performance for both of the top ranked models (AUC = 0.753, SE = 0.026; AUC = 0.754, SE= 0.026) models. None of the model variables had excessive multicollinearity (VIF > 10).

Table 5: Most parsimonious logistic regression models (AIC_c) for tailed frog capture data collected with pitfall arrays at 6 treatments located east of Terrace, BC, in 2012 and 2013. Top ranked models represented 95% of the AIC_C weight.

Model	Rank	k	AIC_c	ΔAIC_c	$AIC_c w$
2012					
distance to stream+densiometer+trap month+site elevation2+days since last rain*	1	9	953.54	0.0	0.506
distance to stream+trap month+site elevation2+days since last rain*†	2	8	953.61	0.1	0.491
2013					
days since last rain+site elevation2*†	1	4	366.15	0.0	0.926
distance to stream+densiometer+trap month+site elevation2+days since last rain*	2	9	373.54	7.4	0.023
orientation+days since last rain	3	6	374.29	8.1	0.016

*Both the linear and quadratic terms were applied to models.

†Most parsimonious model.

During 2013, 3 models explained 96.5% of the AIC_c weight (Table 5). The top ranked model was by far the most parsimonious ($AIC_cw = 0.926$) consisting of covariates for days since last rain and a quadratic term for site elevation. The second ranked model was the same as the top ranked model for the 2012 capture data (Table 5). The most parsimonious model for 2013 was 'good' at predicting the occurrence of tailed frogs (AUC = 0.722 SE = 0.05). None of the variables had excessive multicollinearity (VIF > 10).

In 2012, not all coefficients within the top ranked model were statistically significant. The presence of tailed frogs in traps was negatively correlated with distance to stream, days since the last rain event and the month of August ($p < 0.05$; Table 6). Conversely, tailed frog presence was positively correlated with the time periods of July and October; however, these coefficients were not statistically significant ($p > 0.05$; Table 6). The nonlinear elevation term (linear and quadratic) was positively correlated with the capture of tailed frogs in sites between 440 to 460 m elevations.

All coefficients within the top ranked model for the 2013 capture data were statistically significant ($p < 0.05$; Table 4). Similar to 2012, days since the last rain event was negatively correlated with tailed frog capture. The nonlinear elevation term (linear and quadratic) increased in 2013 and was positively correlated with the capture of tailed frogs between 600 and 620 m.

DISCUSSION

Declines in amphibian populations of the Pacific Northwest may be related to timber harvest in streamside uplands. Understanding the distribution of this Blue Listed species relative to timber harvest, can identify new and evaluate current Best Management Practices (BMP) designed to maintain tailed frogs across human-modified landscapes.

Table 6: Coefficients and measure of statistical significance, including 95% confidence intervals (CI), for covariates from the most parsimonious logistic regression model (Table 5) for tailed frog capture data collected in 2012 and 2013 from pitfall arrays east of Terrace, BC.

Variable	Coefficient	SE	z	*p*	Lower 95% CI	Upper 95% CI
2012						
distance to stream	-0.029	0.006	-4.841	< 0.001	-0.041	-0.017
July	0.287	0.153	1.883	0.06	-0.012	0.586
August	-0.438	0.148	-2.955	0.003	-0.728	-0.147
October	0.151	0.14	1.075	0.282	-0.124	0.425
site elevation	0.014	0.006	2.443	0.015	0.003	0.025
site elevation2	< -0.001	< 0.001	-2.755	0.006	< -0.001	< -0.001
days since last rain	-0.186	0.041	-4.555	< 0.001	-0.266	-0.106
constant	-5.409	1.389	-3.895	< 0.001	-8.131	-2.687
2013						
days since last rain	-0.435	0.119	-3.654	< 0.001	-0.669	-0.202
site elevation	0.034	0.015	2.207	0.027	0.004	0.064
site elevation2	< -0.001	< 0.001	-2.151	0.031	< -0.001	< -0.001
constant	-14.497	4.462	-3.249	< 0.001	-23.243	-5.750

However, the effects of these forest practices often are not evident until years after harvest (deMaynadier and Hunter 1995; Karracker and Welsh 2006; Petranka *et al.* 1993; Kluber *et al.* 2008; Hawkes and Gregory 2012).

Information theoretic approaches for model selection have been relatively underused in the field of herpetology (Mazerolle 2006). Although this approach is robust to bias, the models I tested only represent the data collected at the northern distribution of the species. Those data may be limited by sampling bias that resulted from non-continuous trapping sessions that were most successful when tailed frogs were moving across the study sites. For example, females are highly mobile during the breeding season. Relatively infrequent and discontinuous 6-night trapping sessions could fail to represent that activity in any one year. Similarly, results suggest that a correlation between the timing of trapping session and dry-hot weather would reduce capture rate. Both factors might partially explain the small sample of captured tailed frogs in 2013

Despite the potential for sampling bias, the most parsimonious logistic regression models for both trap years were good predictors of frog activity and distribution. Furthermore, both models contained variables representing temporal, treatment and environmental factors: 1) distance to stream; 2) trap month; 3) site elevation; and 4) days since the last rain event. By exploring the mechanisms that dictate patterns in frog activity, movement, and fine-scale distribution, we can identify land management practices that will aid in the conservation of coastal tailed frogs.

Orientation of movement

Although orientation was not a significant predictor for tailed frog presence in traps, this variable identifies increased activity associated with the specific life stage or requirements of the species. For example, Daugherty and Sheldon (1982) concluded that populations of *A. montanus* were philopatric to streams and that pre-reproductive individuals were the main dispersers. This was because adults remained relatively sedentary (within 40 m of capture), while juveniles were found to make more frequent movements along the stream. For populations of *A. truei* in southern BC, a greater parallel (up and down) movement in relation to the stream edge was observed by Wahbe *et al.* (2000) and Matsuda and Richardson (2005). Upstream travel was greatest in adults while juveniles were captured moving perpendicular to the stream suggesting dispersal.

Populations of *A. truei* in northwestern BC demonstrated a greater tendency to move perpendicular (towards or away) to the larval stream. In 2012, the greatest proportions of tailed frogs were found moving away from the stream (41%). Increased activity resulting in the away orientation was largely attributed to the 31 reproductive females captured in the spring (84% of total captures at that time). Conversely, in 2013 tailed frogs had the greatest proportion of their movement towards the stream (56%). These were males trapped during summer in the forest retention buffer. This movement coincided with a prolonged period without rain (Appendix V).

Wahbe and Bunnell (2001) documented significant downstream movement by larval tailed frogs. In order for populations to remain stable when one life stage is in a lotic habitat, a 'colonization cycle' (Muller 1974) must occur. During 2012, the CPUE for newly metamorphosed individuals was 1.6 times greater for upstream movement post-emergence than any other orientation. This upstream pattern of movement may be instinctual in order to counter the downstream movement by larvae.

Distance of capture from stream

In 2012, distance from stream edge was an important predictor of tailed frog presence within traps. For all age classes, 57% of captures were located in the 5-m streamside arrays. In addition, 82% of adults captured in the forest retention buffer sites were located < 30 m from the stream edge. Similarly, studies in southern BC reported that adult tailed frogs had a greater affinity for areas within 20 m of the stream in clearcuts and mature forests (Matsuda and Richardson 2000; Wahbe *et al.* 2000). This suggests that the fine-scale distribution of tailed frogs in terrestrial habitats can be explained by the location of the maternal stream.

Brosofske *et al.* (1997) reported that the microclimate remains relatively constant up to 31-62 m from the stream edge in forest stands of the Pacific Northwest. This lack of gradient in air temperature, soil temperature, and relative humidity might explain the variation in distribution of tailed frogs observed across my study sites. For example, during 2012 the average temperature in the old growth at the 5-m array was similar to the 80-m array during the spring trapping session (Figure 6).

Capture rates for tailed frogs have been reported to vary according to time of year and sex (Landreth and Ferguson 1967; Brown 1975; Wahbe *et al.* 2004; Hayes *et al.* 2006). Females in northern BC had a greater probability of capture (64% of adults) and were located < 30 m from the stream. This near-stream distribution may be indicative of movements associated with reproduction; females captured at this time were either gravid or post-ovipositioning.

Daugherty and Sheldon (1982) surmised that pre-reproductive individuals of *A. montanus* undergo dispersal to locate food, shelter or new breeding grounds. Individuals dispersing from degraded or high-density areas can potentially find higher quality or more available habitat (deMaynadier and Hunter 1999), but may experience greater mortality than sedentary individuals (Rappole *et al.* 1989). Similar to southern populations of *A. truei* (Matsuda and Richardson 2005; Wahbe *et al.* 2004), a greater proportion of juveniles were found in traps at the 55-m arrays for old growth and clearcut treatments.

Bury and Corn (1991) suggested that tailed frogs emerge in the fall. In northwestern BC, metamorphs were often trapped in streamside arrays during October (Figure 10). Furthermore, of the 11 metamorphs captured in the clearcut, 7 individuals were newly metamorphosed individuals captured in arrays ≤ 30 m from the streamside (Figure 9). Newly metamorphosed individuals may be more sensitive to ecological and physiological constraints relative to other life-stages (deMaynadier and Hunter 1999). Limited perpendicular movement from the stream edge is likely caused by a more suitable near-stream microclimate (Brosofske *et al* 1997).

Forest retention treatment

Similar to studies on southern populations of tailed frogs (Wahbe *et al.* 2004, Matsuda and Richardson 2005; Hawkes and Gregory 2012), adults were more abundant (43% of total captures) in mature stands and decreased as canopy overstory was reduced (Figure 9). Although the treatment type was not significant in the model predictions, the variable identifying canopy closure at the trap array (densitometer), suggests that overstory cover is important in predicting tailed frog presence (Table 5).

Previous studies for southerly populations of *A. truei* have reported that larvae in clearcuts undergo earlier metamorphosis (3-4 years) and are found at higher densities (Richardson and Neill 1998; Wahbe and Bunnell 2001; Wahbe *et al.* 2004). However, this habitat type could act as an ecological sink, as newly metamorphosed individuals may be more sensitive to ecological and physical constraints relative to other life-stages (deMaynadier and Hunter 1999). Although newly metamorphosed individuals existed in the clearcut treatment, few were captured in arrays further than streamside (Figure 9), identifying the importance of the near-stream microclimate for ameliorating the physiological constraints of this life stage. Additionally, a greater number of metamorphs, but fewer adults within clearcuts could be the result of either low recruitment of metamorphs to adulthood or greater post-metamorphic dispersal from this habitat type (Wahbe *et al.* 2004). This may explain why fewer adults and a greater CPUE for metamorphs existed within this forest retention type compared to the old growth, forest retention buffer or regeneration treatments.

Temporal patterns of movement

Quantifying seasonal variation in the movement of terrestrial tailed frogs can increase our understanding of dispersal and population connectivity as well as seasonal habitat requirements. Where studied, the seasonal movements of *Ascaphus* have varied among species and populations. For *A. montanus*, Daugherty and Sheldon (1982b) found no difference in the direction of movements across seasons. However, Matsuda and Richardson (2000) noted that the greatest rate of movement for coastal populations of *A. truei* in southern BC occurred during spring and fall. Others have proposed that breeding results in annual migration (Landreth and Ferguson 1967; Brown 1975; Wahbe and Bunnell 2001; Wahbe *et al.* 2004; Hayes *et al.* 2006); however, little or no data has been provided to support this prediction.

Trapping data from this study suggests that increased seasonal movements correlate with the species breeding phenology. Specifically, movement to ovipositioning habitats were observed during June and July. Gravid females were caught moving towards or up the larval stream in early June 2013 in the Kleanza sites. Furthermore, the majority of adults traveling away from the stream in July 2012 were females that had deposited eggs. Of the 23 adult frogs captured in October, 2012, 9 females were gravid and 9 males had darkened breeding pads. In 2013, 6 adult frogs were captured in October with 4 gravid females and 1 male in breeding condition. These data suggest that in northwestern BC breeding begins in the late fall – something confirmed by direct observation (McEwan Pers. Obs.).

Similar to Matsuda and Richardson (2000), I observed a negative correlation between tailed frog captures and the summer trapping session. In 2013, however, captures increased by a magnitude of 1.56 during the summer compared to the spring. This movement and the subsequent captures may have been a response to a prolonged period of no rain (> 13 days; Appendix V). The majority of captures (64%) were adults within the forest retention buffer and the regeneration sites moving towards the stream.

With the onset of fall, the number of tailed frogs captured in pitfall arrays increased. Cool temperatures (< 11°C) and moderate to heavy rain events < 1 day apart increased tailed frog movement. For example, 8 metamorphs in 2012 were moving upstream (Figure 8) potentially to overwintering habitat while 15 individuals were located at arrays ≥ 30 m (Figure 9).

Metamorphosis of populations in Washington and Oregon occurred during a brief time period in late summer (Bury and Adams 1999). Data from this study documented emergence from the larval stream beginning in late August with the majority of captures occurring in mid-October (Figure 10). This would suggest that metamorphic emergence at the species' northern range extends into the fall.

Elevation

Trapping success, thus, the activity and movement of tailed frogs, was correlated with the elevation of the study sites. Amphibians found at high elevations have adapted to a colder thermal regime, but have physiological constraints that limit activity to a relatively narrow range of temperatures (McCaffery and Maxell 2010). In this study area, elevation is strongly correlated with the onset of the snow-free period and associated warmer air temperature. Thus, the timing of ovipositioning, metamorphosis and breeding in addition to post-winter emergence and activity is related to the elevation at which the population (i.e., study site) is located.

As of June 1, 2012, there were still significant snow packs (195% of normal) within watersheds of the Skeena River Basin (BC River Forecast Centre 2012). Sites below 528 m were snow free by the end of May and had earlier emergence from overwintering locations than sites above 650 m where presence was not detected until mid-July. The majority of captures during 2012 were at 463 m. Conversely, by the beginning of June 2013, snow indices were well below normal, suggesting that melt was 1-2 weeks earlier than normal (BC River Forecast Centre 2013). The first tailed frogs were observed by the end of May when sites were accessible. The majority of captures in 2013 occurred at 650 m.

Capture data suggests that the timing of emergence, ovipositioning and breeding is dependent on the start of the snow-free period. In BC, temperatures are expected to increase (0.5°C per decade) with the northern portion warming faster. An increase in winter precipitation as rainfall and a decline in summer stream flow for snow-dominated water systems are also predicted (BCMWLAP 2002; Hamann and Wang 2006). This alteration of temperature regime and stream flow may affect the behavioural patterns and quality of terrestrial and aquatic habitat for the tailed frog in northern BC.

CONCLUSION

Drawing on the existing literature, I tested 3 predictions to describe and explain the fine-scale distribution and movement of the tailed frog at their northern extent in western BC. Juveniles were more commonly located in arrays ≥ 55 m from the stream edge in both the old growth and clearcut harvested sites, suggesting that juveniles are dispersing from high density or degraded habitats. Additionally, movement patterns of reproductive aged tailed frogs did correspond with key reproductive periods. For example, during the spring, 34 females were captured displaying recent signs of breeding (i.e., gravid or post-ovipositioning) and 59.5% of adult females were captured in 5-m arrays next to the larval stream. This supports my prediction that movement patterns and the probability of capturing females are related to reproductive events. Tailed frogs were more commonly located in traps following rain events (< 1 day) and when temperatures remained below the thermal maxima (26.5°C). Thus, pitfall traps are best at quantifying population distribution and relative abundance when tailed frogs are active and demonstrating above-ground terrestrial movements.

Similar to studies in southern BC, the populations of tailed frog I studied were most likely to be captured < 20 m from the stream edge regardless of forest retention type. This refutes my prediction that tailed frogs in old growth habitats would be captured at greater distances from the stream edge. However, this result may simply reflect a behavioural preference for stream-side habitats by ovipositioning females and emerging metamorphs, regardless of canopy closure. The capture rate of adults did decrease as overstory was reduced suggesting that forest harvesting does alter the distribution of this age class within a treatment.

Although pitfall traps can be useful for assessing temporal patterns of behaviour, capture rates are likely sensitive to the trapping schedule. For example, had trapping occurred earlier in 2012, the emergence of post-ovipositioning females from the larval stream may have been lower as was the case in 2013. For this technique to fully represent the seasonal ecology of tailed frog, a more continuous duration of trapping is necessary. Furthermore, more continuous trapping would address temporal effects associated with weather (e.g., rain, heat wave, or drought) that influence frog movement and capture success. Because of time constraints, I only monitored the traps at each site for one 6-night period at 3 times during the growing season (May-October). However, when comparing the capture success of my study to previous works on southerly populations, total numbers were similar. For example, over 3 years of trapping, Wahbe (2003) captured 254 tailed frogs; while Matsuda (2001) captured 175 tailed frogs over 2 years.

RECOMMENDATIONS

Managing forests for the tailed frog

Tailed frog research has focused on the impacts of forest practices relative to larval development and aquatic habitat (Corn and Bury 1991; Wallace and Diller 1998; Wahbe and Bunnell 2001) with few recent studies considering the post-metamorphic life stages (Wahbe *et al.* 2004; Matsuda and Richardson 2005; Burkholder and Diller 2007; Hawkes and Gregory 2012). Compared to most other anurans, tailed frogs are less tolerant of warm temperatures and prone to desiccation. Thus, the species requires cold mountain streams and complex vertical and horizontal wood structure that is typically found in old forests (Aubry and Hall 1991; Corn and Bury 1991; Dupuis and Waterhouse 2001; Kluber *et al.* 2008; Hawkes and Gregory 2012). When managing forests for this species, it is important to understand how post-metamorphic tailed frogs are distributed in relation to life-stage and the corresponding requisite environmental conditions.

During 2013, temperatures were warmer and snow pack melted faster, triggering earlier emergence from over-wintering sites and ovipositioning. This was evident from fewer gravid or post-ovipositioning females captured during the spring. The majority of tailed frogs captured over the two years were in the 5-m arrays, closer to rain events (< 1 day) and when air temperatures were < 26.5°C. Furthermore, tailed frogs were captured within each timber forest retention treatment, but as overstory declined, the number of captures decreased with an increasing distance from the stream. These results confirm past work noting the relationship between the distribution and activity of tailed frogs relative to micro-site or broader climatic conditions, and the need for intact overstory and complex forest structure (Daughtery and Sheldon 1982; Matsuda and Richardson 1999). Wahbe *et al.* (2004), for example, reported that relative to clearcuts, tailed frogs in old growth forests were distributed farther from the larval stream. Furthermore, results of my study confirmed the prediction that tailed frogs will demonstrate more active and dynamic movement and distribution when weather conditions (e.g., rainfall events) are suitable for above ground terrestrial movements.

One approach for maintaining post-metamorphic tailed frogs across managed forest stands is the designation of riparian reserves (buffers; Bull and Carter 1996; Dupuis and Steventon 1999). Within this study, treatments with approximately 50-m retention buffer had similar abundance of tailed frogs (adults, juveniles and metamorphs) as the old-growth treatments. In addition, the distribution of captured tailed frogs across all treatments was greatest within an area ≤ 30 m from the edge of the larval stream. These data suggest that a buffer of insufficient size (< 50 m) will potentially exclude habitat typically used by tailed frogs.

The Forest Practices Code Act of BC identifies two riparian zones within the Riparian Management Area: 1) riparian reserve zone where harvesting is not permitted and 2) riparian management zone where constraints to harvesting exist. These zones now serve as guidance under the Forest and Range Practices Act. However, there is no regulatory requirement for a riparian reserve zone around smaller non-fish bearing streams typical of the headwater systems where breeding populations of tailed frogs are found. Within these streams, bank vegetation is left undisturbed if it is < 10 m from the stream edge and deemed to be non-merchantable (BC Ministry of Forests and Ministry of Environment 1995). In addition, the riparian management zone that may exist on these smaller streams is 20-30 m from the stream edge and places minimal constraints on timber harvest practices. The results of this study suggests that a < 20 m riparian management zone with minimal constraints to harvesting and a lack of a riparian reserve zone are not suitable for populations of tailed frogs in northwestern BC.

There is no consensus on the amount of standing timber that should be retained as a buffer for stream obligate amphibians. Olson and Rugger (2007) suggest that a 6-76 m harvest buffer would retain amphibian populations found in small streams adjacent to stands in the Pacific Northwest that were harvested using moderate thinning practices. Stoddard and Hayes (2005) suggest that riparian reserve zones around small streams adjacent to clearcuts should be > 46 m to retain stream amphibians. Similarly, Perkins and Hunter

(2006) report that in Maine, buffers between 23-35 m are not adequate for maintaining riparian salamanders at an abundance comparable to non-harvested sites. Furthermore, Young (2000) suggests that a riparian reserve of 70-90 m would allow for riparian-stream linkages with downed wood, litter, bank stability and suitable microclimate. Marsh and Trenham (2001) suggest that the maximum observed distance traveled by an amphibian species from the stream should serve as the minimum width of a riparian reserve zone. The maximum distance traveled accounts for the nature of incomplete sampling in most long-distance movement studies.

Riparian reserves should be established for tailed frogs around important streams and breeding areas (BCMWLAP 2004). The following 3 criteria would ensure that the reserves accommodate both the larval and terrestrial life stages: 1) the reserves should include the area near streams most likely to be used by tailed frogs on a seasonal basis and be at least 20 m; and 2) a riparian management zone should extend past the reserve zone and be large enough to ameliorate edge effects; and 3) management zones should be used to maintain connectivity between reserves (BCMWLAP 2004; Spears and Strofer 2008). Maintaining functional riparian reserves and managing upland forest as habitat for tailed frogs will ensure the continuance of upstream movements by metamorphs and females to headwaters, increasing dispersal and gene flow. Furthermore, the retention of riparian areas will increase the total area of habitat for resident tailed frogs and act as a corridor for within site movement and dispersal.

CHAPTER 3

HABITAT SELECTION BY THE COASTAL TAILED FROG OF NORTHWESTERN BC

INTRODUCTION

Historically, conservation studies and efforts have focused on vascular plants, birds mammals or fish, but not on cryptic or nonmarket species (Griffiths and Dos Santos 2012). In North America, the US Endangered Species (1973) and the Canadian Species at Risk (2004) Acts, have resulted in the formal consideration of nongame species (Semlitsch 2002). Unfortunately, a bias still exists for a number of taxonomic groups, specifically amphibians, who receive relatively little attention (Griffiths and Dos Santos 2012). Current conservation strategies for terrestrial mammals and birds are insufficient for amphibians, a taxon that is declining globally (Houlahan *et al.* 2000; Dodd 2009). Because amphibians require both aquatic and terrestrial environments (Semlitsch 2002), conservation efforts and practices must target their biphasic life history.

Although scientists agree that a number of factors are contributing to the extirpation or extinction of amphibian species, the most wide-spread cause is believed to be habitat alteration (Houlahan *et al.* 2000; Semlitsch 2002; Cushman 2006; Dodd 2009). Habitat is lost or altered by draining and filling wetlands, channelizing streams, creating impoundments, and removing native vegetation. Fortunately, these causal processes can be identified, minimized, and even reversed. Given the scope of threats to amphibian species, habitat alteration is relatively easy to address through land-use planning and the protection of habitat (Semlitsch 2002). Such strategies first require a better understanding of the interactions between land use and the ecological and physiological requirements of the focal amphibian species.

Information describing distribution and movement is necessary to understand the ecology of a species. For example, many amphibians use aquatic sites for breeding and as a developmental environment for larvae whereas adults are found in terrestrial habitats. Thus, distributional patterns can reflect age-specific variation in ecological requirements (Daugherty and Sheldon 1982). However, our knowledge of the spatial ecology of many amphibian species during the terrestrial life stage is limited (Rowley and Alford 2007). Terrestrial habitats may be critical for maturation and ultimately reproduction by adults, but are overlooked during conservation planning.

There is a well-established empirical relationship between the area and ecological characteristics of forest cover and the occurrence of many amphibian species (Dupuis and Steventon 1999; Ascaphus Consulting 2003; Wahbe *et al.* 2004; Matsuda and Richardson 2005). For example, Nuzzo and Mierzwa (2000) found that the greatest abundance and diversity of amphibians were in forests that retained 'natural' characteristics including overstory, ground level vegetation, and coarse woody debris. Others have reported a negative response of amphibian populations to anthropogenic activities such as roads (Farhig *et al.* 1995; Gibbs 1998) or timber harvest (Welsh and Ollivier 1998; deMaynadier and Hunter 1998, 1999; Dupuis *et al.* 2000; Chan-McLeod 2003; Hawkes and Gregory 2012). As an example, Johnston (1998) found that timber harvest restricted the movement and altered the use of habitat by the Pacific giant salamander (*Dicamptodon tenebrosus*).

Previous research in the Pacific Northwest has established that amphibians are sensitive to forest management practices (Perkins and Hunter 2006). Additionally, amphibian abundance has shown a positive correlation with the structure and complexity of forest stands related to harvest history (Aubry and Hall 1991; Corn and Bury 1991; Wahbe *et al.* 2004). For example, Maxcy and Richardson (1999) concluded that 4 salamander species responded negatively to forest harvesting because of a loss of stable climatic conditions (e.g., temperature and humidity) that old growth stands provide. Amphibians require habitats with high moisture and a narrow range of temperatures (Palis 1997, 1998; deMaynadier and Hunter 1998; Chan-McLeod 2003; Baldwin *et al.* 2006; Perkins and Hunter 2006). In the case of southerly populations of the coastal tailed frog (*Ascaphus truei)*, Matsuda and Richardson (2005) concluded that adults were less abundant in clearcuts; however, movements or the distance traveled from stream was not influenced by forest harvest. Additionally, Hawkes and Gregory (2012) concluded that the abundance of tailed frogs was negatively affected by upland logging 10 years post-harvest.

In BC, many populations of amphibians are at risk because of anthropogenic activities, including urban development, environmental contamination, logging, and water impoundment. These threats have resulted in ~ 25% of the amphibian species in the province to be listed as Endangered or Threatened (BC Environment 2002). The coastal tailed frog is on the provincial Blue List and as a species of Special Concern under the Federal Species at Risk Act (SARA). This species is susceptible to threats from urban development, timber harvest, and independent power projects (IPP). These activities remove canopy overstory, reduce coarse woody debris, and can impact water quality and flow within larval streams. The majority of research and inventory studies of the coastal tailed frog have considered the distribution and habitat requirements of the larva (Wahbe 1996; Wallace and Diller 1998; Bury and Adams 1999; Dupuis *et al.* 2000; Ritland *et al.* 2000; Wahbe and Bunnell 2001). Until recently, few studies have focused on the ecology of the terrestrial stage of the species (Wahbe *et al.* 2004; Matsuda and Richardson 2005; Hayes *et al.* 2006; Burkholder and Diller 2007) and none have investigated the ecology of this species at the northern extent of its range.

CHAPTER PREDICTIONS

In this chapter, I investigated environmental factors that influenced resource selection, movement, and distribution of adult tailed frogs across a range of terrestrial habitats affected by timber harvest. I used site and environmental data collected at the patch (micro-habitat) and forest stand (macro-habitat) scales to quantify resource selection of adult frogs monitored with radio telemetry. I tested 3 predictions that were supported by existing literature and our general understanding of the habitat ecology of forest-dependent amphibians.

Forest structure and resource use – I predicted that the distribution of tailed frogs would be positively associated with habitat features that ameliorate variability in climate, increase availability of food resources and provide protection from predators; this reflects previous studies identifying the importance of downed wood and other subterranean structures as habitat for amphibians.

Temporal, climate and resource use – I predicted that during warmer and drier portions of the year, tailed frogs would select locations close to a stream and with habitat features, such as coarse woody debris, that provided protection from thermal stress and dehydration; this reflects previous work identifying the importance of thermal and hydric-regulation.

Forest retention treatment and resource use – I predicted that as forest overstory declined, tailed frogs would have a greater association with habitat features, such as moist microsites or coarse woody debris that maintained physically suitable microclimates.

METHODS

Study Area

The study area was situated on the leeward side of the Coastal Mountains in northwestern British Columbia. Vegetation communities included the Coastal Western Hemlock (CWH) and the Interior Cedar-Hemlock (ICH) Biogeoclimatic Ecosystem Classification zones (Meidinger and Pojar 1991). The CWH had mild temperatures and heavy rainfall with climax forests of western hemlock (*Tsuga heterophylla*) and amabilis fir (*Abies amabilis*). The ICH, reflective of a transitional climate between coastal and interior stands, contained climax forests of western hemlock and subalpine fir (*Abies lasiocarpa*). The main disturbance across these study sites was timber harvest. See Chapter 1 for a more detailed description of the study area.

I collected radio telemetry data during 2011 and 2012 for 24 adult tailed frogs across 3 watersheds: 1) Gosling (GO); 2) Ascaphus (AS); and 3) Kleanza (KL). Sites in each watershed were classified as 1 of 3 categories representing forest harvest history: 1) mature second growth or no history of harvest; 2) harvested, but with habitat retention of 30-50 m from the edge of the larval stream (i.e., forest retention buffer); and 3) harvested with minimal to no overstory canopy. The GO sites were located within the transition zones between the CWHws and the ICHmc2 (Meidinger and Pojar 1991). Study sites were classified as CWHws1 or CWHws2 and situated at relatively low elevations (319-463 m above sea level (asl)). Where forested, these sites were dominated by old (> 250 years) western hemlock and amabilis fir. Within the understory, moist pockets of devil's club (*Oplopanax horridus*), skunk cabbage (*Lysichiton americanus*) and abundant *Vaccinium* species existed. Most harvesting in this watershed occurred recently (< 5 years) resulting in no tree canopy and the substantial growth of fireweed (*Chamerion angustifolium*) and bracken fern (*Pteridium aquilinum*.

Similarly, the AS watershed was located at low elevations (319-582 m asl) within the transitional zone between the CWHws and the ICHmc2 (Meidinger and Pojar 1991). Study sites were classified as CWHws1 and situated at low elevations (273-582 m asl). Where forested, these sites were dominated by old (>140 years) western hemlock and subalpine fir with some western red cedar (*Thuja plicata*) and Sitka spruce (*Picea sitchensis*). Within the understory, moist pockets of devil's club and skunk cabbage were present amongst abundant *Vaccinium* species and false azalea (*Menziesia ferruginea*). Most harvesting in this watershed occurred 10-15 years in the past resulting in the regeneration of dense stands of western hemlock and lodegepole pine (*Pinus contorta*) < 10 m tall.

The sites within the KL watershed were found within two variants of the Coastal Western Hemlock BEC zone (CWHws2, CWHws1). Two sites were located at higher elevations (650 m and 801 m asl; CWHws2). The old growth treatment had > 250 year old western hemlock, amabilis and subalpine fir in a multi-storied canopy; while the forest retention treatment contained 50 m of > 250 year old western hemlock, amabilis and subalpine fir along the stream. Both treatments contained moist pockets with abundant devil's club and skunk cabbage in the understory. The third site was lower in elevation (528 m asl; CWHws1) and had dense regeneration of western hemlock and lodgepole pine < 20 m tall. This site was harvested in 1987 and had poorly developed understory with moist pockets of devil's club and lady fern (*Athyrium filix-femina*).

Data Collection

Animal capture and radio telemetry – Adult tailed frogs were captured using 3 methods: 1) pitfall traps; 2) systematic visual encounter surveys (VES); and 3) incidental captures. Frogs were captured during July-October, 2011 in the AS and KL sites using non-systematic visual searches of riparian forests adjacent to known larval streams. In 2012, pitfall traps were opened for a total of 5,184 hours (Chapter 2). The VES consisted of 3 consecutive survey days in each site during the spring, summer and fall of 2012. A total of 15 person-hours were completed per site during each VES. Incidental captures occurred in both years.

When captured, tailed frogs were identified as male or female and measured for snout vent length (SVL), shank length (SL) and weighed to the nearest 0.01 g. Only individuals > 5.5 g were fitted with Very High Frequency (VHF) radio transmitters (8-10% of body weight) and relocated for 5-24 days. I used BD-2N (0.45 g) and BD-2X (0.34 g) transmitters in 2011 and 2012, respectively (Holohil Systems Ltd. Carp, Ontario). To attach the transmitter, I used a belly-belt system (Muths 2003) consisting of Gossamer Floss™ jewelry cord (B. Toucan Inc., USA) and Japanese glass seed beads (olive green, size 15, Figure 11). In total, the belt and transmitter weighed approximately 0.54 g and 0.46 g, for the respective transmitter models, with a nominal lifespan of 13-22 days. Of the 24 individuals followed, no mortality was documented; however, the fates of 7 individuals were unknown due to tag failure (n = 4) or an inability to recapture and remove the tag (n = 3).

I used a hand-held receiver (R-1000 Communications Specialist Inc., Orange, CA) to relocate each telemetered tailed frog once per day.

Figure 11: VHF radio transmitter (2) with belly-belt attachment (1) and antenna (3) used to relocate coastal tailed frogs.

Daily relocations were conducted between 7 am and 9 pm and staggered so that at least 15 hours had passed between consecutive relocations. I concluded the search when I had visual confirmation of the individual. When tailed frogs were located within or under debris, I used multiple triangulation points and signal strength to identify the relocation with a high level of confidence.

Statistical Methods

Data analysis

I used resource selection functions (RSF) to relate the locations of monitored tailed frogs to 9 independent variables measured at two spatial scales (Table 7). An RSF can be calculated using a number of statistical techniques (Johnson *et al.* 2006). I used conditional fixed-effects logistic regression as this method provided a more sensitive measure of resource availability, controlling for temporal variability in the availability of resources, as use locations are paired with available locations sampled from an ecologically relevant area (Johnson and Gillingham 2005).

I collected resource data at the observed location of the tailed frog (used habitat) and a paired random location (available habitat; Manly *et al.* 2002). Random locations were selected according to a random direction and distance (3-20 m) centered on the most recent location of the tailed frog. Few studies have documented the mean daily movements of tailed frogs (Wahbe *et al.* 2004; Maxcy 2000), thus, I inferred a minimum distance from previous research for a related species (*Leiopelma* spp.; Cree 1989; Newman 1990). To prevent the macro-habitat sampling plots (100 m^2) of the paired random locations overlapping with the used locations, I added 11.28 m to each random distance (Figure 12).

Spatial scales

I collected resource data at two spatial scales using nested plots centered over the used or available locations (Figure 12). The micro-habitat scale (Mi; 1-m^2 plot), represented the environmental variables assumed to influence the distribution of monitored tailed frogs relative to fine-scale physiological constraints (e.g., temperature and light). At the macro-habitat scale (Ma; 25-m^2 plot), measured variables accounted for stand-level forest attributes (e.g., site moisture, tree species, CWD volume, and percent canopy opening).

Micro-habitat variables – At each tailed frog and paired random location, I measured light intensity (lux; Extech Light Meter) and microclimate (air temperature (°C) and relative humidity (%); Kestrel 4500 weather meter). I used a Gaussian term to represent the nonlinear effect of temperature on the distribution of monitored frogs. This equation consisted of both the linear component, identifying the increase in the relative probability of use of a site, and a squared component to identify where the relative probability of use decreases as a function of increasing temperature.

Macro-habitat variables – Each habitat plot was classified as 1 of 3 categories according to the distance of the array from the clearcut (hard) edge: 1) located between the stream edge and > 10 m from the clearcut edge; 2) ≤ 10 m on either side of the hard edge; and 3) > 10 meters from the hard edge within a clearcut. I used a spherical densiometer to quantify the percent canopy closure above each location.

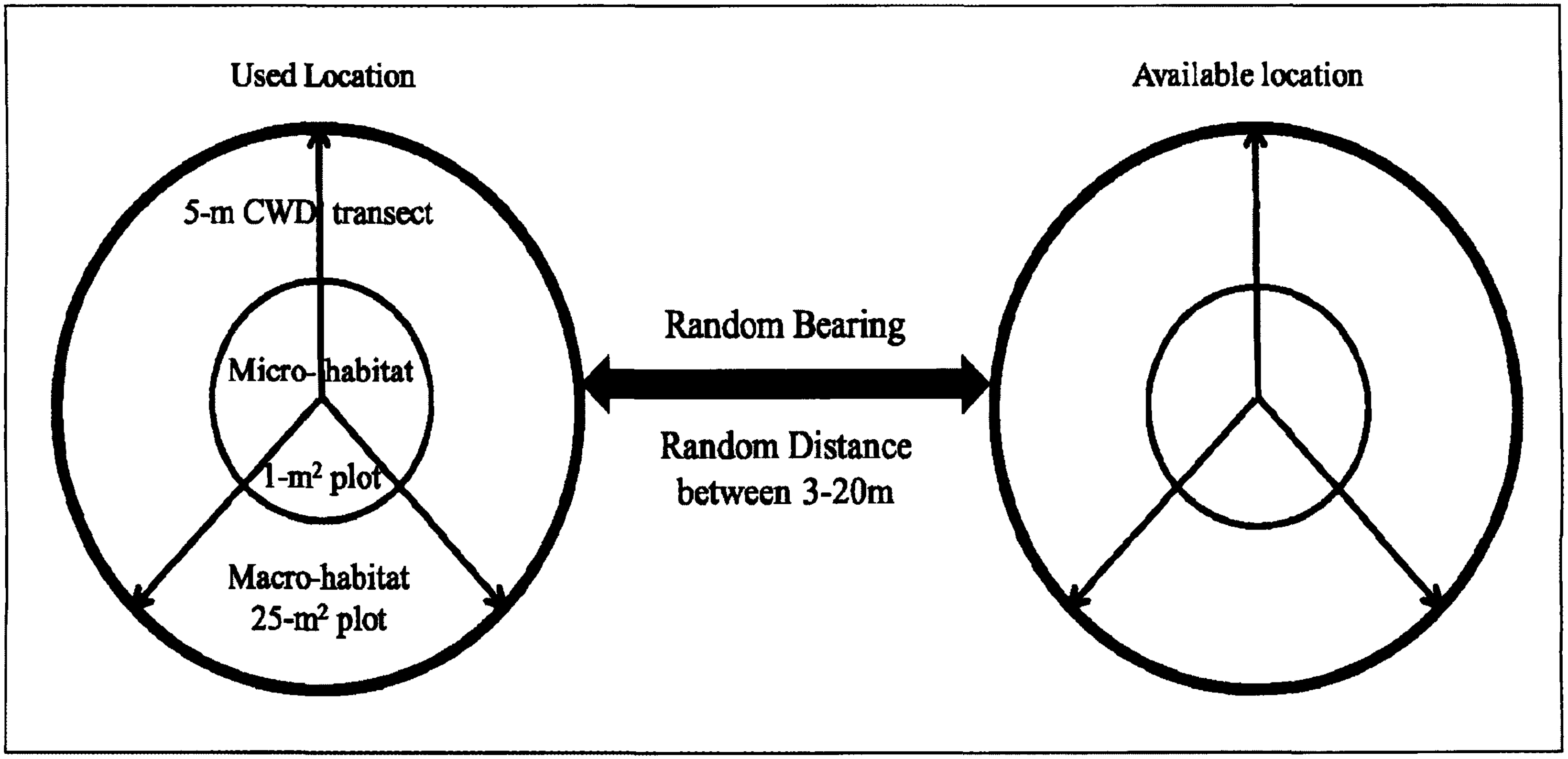

Figure 12: Illustration of the nested sampling design for recording habitat characteristics at used and available locations for tailed frogs at the micro- (1-m^2 plot) and macro-habitat (25-m^2 plot) scales. Arrows represent the 5-m coarse woody debris transect lines.

I centered a 100-m^2 plot (5.64-m radius) on each location. The depth of the organic layer was identified to the nearest 0.1 cm (BC MELP 1998). Additionally, I measured tree diameter at breast height (dbh), vigor (living or dead), number of root hollows, and the Wildlife Tree Classification (BC MELP). Root hollows were openings at the base of a tree where resources such as food, security, or refuge habitat could exist. These openings had to enter the tree cavity to a depth of 5 cm and could be found within any living or dead standing tree. Openings were classified as 1 of 3 categories: 1) < 10cm; 2) > 10cm; and 3) both sizes and quantified based on the total number present within a location.

Within each plot I assessed the amount and composition of CWD along 3 5-m transects oriented $> 120°$ from an initial random bearing for a total line length of 15 m at each location (Figure 12). I measured the length, decay class and species for each piece of CWD ≥ 7.5 cm in diameter that was intercepted by a transect. I condensed the 5 classes of CWD adopted by the BC MELP (1998) into 3 decay classes: 1) contained pieces that still retained shape and could be identified to species; 2) contained pieces that had bark sloughing and heartwood was beginning to soften; and 3) contained pieces that were decomposed and laying on the forest floor or had vegetation beginning to grow within the log. Using Van Wagner's (1968) equation, I quantified the CWD volume by decay class at each location:

$$V= (\pi^2/8L)\sum d^2$$

where V is the volume per unit area (m^3/m^2), L is the length of transect (m), and d is the diameter of the log at the intercept (m).

I used the Ecosystems of BC (Meidinger and Pojar 1991) for the Prince Rupert Forest Region and indicator plant species within the 25-m^2 plot, to quantify site moisture as: 1) 'dry' if no species associated with wet ecosystems were present; 2) 'mesic' when devil's club was

< 10% with minimal oak fern (*Gymnocarpium dryopteris*); 3) 'subhygric' when < 20% devil's club was present and dominant in oak fern; and 4) 'hygric' when the site had > 20% devil's club and was dominated by lady fern or trees with affinity for wet soil (e.g., *Salix* spp.).

Model selection and evaluation

I used Akaike's Information Criterion for small samples (AIC_c) to rank and select the most parsimonious model representing the resource selection of monitored tailed frogs. I used Δ AIC_c to identify the 'best' model in each of the sets and Akaike weights ($AIC_c\, w$) to quantify model selection uncertainty. If models were nearly equivalent (i.e., Δ $AIC_c < 2$), then I selected the model with the fewest number of parameters (Johnson *et al.* 2006). To control for potential differences in resource selection between gender, I developed model sets using locations from the female (n = 16 individuals) and male (n = 8 individuals) tailed frogs. Also, I pooled all locations and developed a set of models that represented the general resource selection patterns of the sample of tailed frogs that I monitored.

I calculated the Area Under the Curve (AUC) for the Receiver Operating Characteristics (ROC) to test the predictive performance of the most parsimonious models. The curve represents the proportion of correctly and incorrectly classified predictions over a continuous range of probability thresholds from 0 to 1.0 (Pearce and Ferrier 2000). Scores of 0.5-0.7 suggest a poor model, 0.7-0.9 a good model, and 0.9-1.0 a highly predictive model (Swets 1988). When performing the ROC test, I withheld paired used and available sites sequentially from the model building process and then used that withheld data to generate a predicted probability. Thus, a bootstrapping-like process resulted in an independent evaluation of the predictive performance of the logistic regression model.

Table 7: Independent variables used to derive RSF models for the coastal tailed frog in northwestern BC at the micro- (Mi) and macro-habitat (Ma) scales.

Variable	Variable Description
Macro-habitat	
distance to edge	Distance of trap arrays from hard edge: 1) locations from stream edge to < 10m from hard edge; 2) locations ± 10m of the hard edge; and 3) locations > 10 meters from a hard edge.
distance to stream	Straight-line distance from the larval stream edge.
densiometer	Percent canopy opening.
site moisture	Inferred site moisture based on indicator plants in the 25-m^2 plot: 1) dry; 2) mesic; 3) subhygric; and 4) hygric.
CWD volume	Calculation of CWD volume for 3 decay classes using Van Wagner's (1968) equation.
litter	Depth (cm) of the organic horizon (litter, fermented and humus; LFH) and duff layer.
root hollows	Number of openings at base of tree: 1) < 10cm; 2) > 10cm; and 3) both sizes.
Micro-habitat	
temp*	Temperature (°C) at location
humidity	Relative humidity (%) at location
light	Light intensity (lux) at location

* Variable had Gaussian term applied to represent a non-linear relationship.

I used 95% confidence intervals to assess the relative strength of selection or avoidance for each of the covariates within the most parsimonious model. When intervals do not overlap zero, covariates are considered as a significant factor influencing the distribution of tailed frogs. I used a modified variance estimator to statistically control for autocorrelation that might be expected from the repeated sampling of locations from a monitored tailed frog (Williams 2000; Nielson *et al.* 2001). I used variance inflation factors (VIF) to test for multicollinearity among model covariates for the tested models. If a variable had a VIF value > 10 or a mean VIF value for the model > 1.0 it was removed from the model (Chatterjee *et al.* 2001). All statistical analysis was conducted using Stata (ver.12.1, StataCorp LP, 2012).

Patterns of movements

I calculated the 90% minimum convex polygon (MCP) for 17 tailed frogs with ≥ 10 locations (Arcview 3.2, Animal Movement Analysis extension). A MCP is the smallest polygon that would represent the boundary locations of an individual's movement during a monitoring period (Hayne 1949). The estimated area of use represents the short-term daily activity of the individual over the period of monitoring. Given the limited period of monitoring for each frog, the area of use could be influenced by short-term seasonal behaviours such as migration to access breading locations.

RESULTS

Radio-telemetered animals

In 2 years of radio telemetry, a total of 24 adult tailed frogs (16 females; 8 males) were followed between 5-24 days (mean 10.75 days, SE = 0.89) for a total of 573 used and paired locations. Females were on average larger (Chapter 2) and the mean tag weight for both genders was rarely outside of body weight guidelines of 5-8% (n = 3 ≥ 8.00% body weight;

Richards *et al.* 1994). Of the 24 tailed frogs, 11 were in the old growth (6 females; 5 males); 10 in the forest retention buffer (7 females; 3 males); and 2 females were monitored in the clearcut treatment (Table 8). No mortality was documented; however, the fates of 7 individuals were unknown due to tag failure (n = 4) or an inability to recapture and remove the tag (n = 3).

Gender differences in movement and space use

The distance moved between daily relocations ranged from 0-45.7 m for all frogs ((mean 5.49 m, SE = 0.53). Generally, female frogs had greater daily movements when compared to males (females: 73.6 m, SE = 17.4; males: 41.0 m, SE = 9.5; Figure 13). The MCPs for individual frogs were between 116 to 3386 m^2 with a mean estimate of 628.12 m^2 (SE = 190.04). Tailed frogs relocated in the old growth had larger estimates of space use (977.50 m^2, SE = 368.65) than those in the forest retention buffer (320.57 m^2, SE = 92.37) or clearcut treatments (307 m^2, SE = 71.00); however, the clearcut estimates were based on 2 individuals. Females had larger mean estimates of space use compared to males (730.50 m^2, SE = 317.33; 481.86 m^2, SE = 109.83).

Forest retention treatment

Adult tailed frogs monitored in the old growth treatment traveled 23 m further from the origin of capture compared to the clearcut and forest retention buffer (77.1 m, SE = 22.8; 54.3 m, SE = 19.2; 40 m, SE = 8.1, respectively); however, only the old growth and the forest retention buffer treatments differed significantly (Figure 14). Additionally, adults had the greatest daily movement rates in the old growth (7.4 m/day, SE = 0.8) compared to the clearcut (5.2 m/day, SE = 2.0) and forest retention buffer treatments (3.7 m/day, SE = 0.8).

Table 8: Telemetry data for 24 adult tailed frogs identifying the average number of days followed, weight (grams) and the percent body weight of the tag for each forest retention treatment in 3 watersheds located east of Terrace, BC, during 2011 and 2012. Numbers in brackets are standard errors (SE).

Forest retention treatment	Total captures	Average days monitored	Average weight	% body weight
Old growth	11	10.27 (1.67)	9.67 (0.57)	6.14 (0.42)
Female	6	9.67 (3.07)	9.92 (0.71)	5.7 (0.31)
Male	5	11.00 (1.00)	7.18 (0.15)	7.42 (0.27)
Forest retention buffer	11	10.91 (1.02)	9.79 (0.79)	5.86 (0.50)
Female	8	10.38 (1.32)	10.91 (2.18)	5.00 (0.29)
Male	3	12.33 (1.20)	6.82 (1.74)	8.15 (0.33)
Clearcut	2	12.5 (1.5)	10.08 (0.74)	4.90 (0.56)
Female	2	12.5 (1.5)	10.08 (0.74)	4.90 (0.56)
Male	0	0	0	0

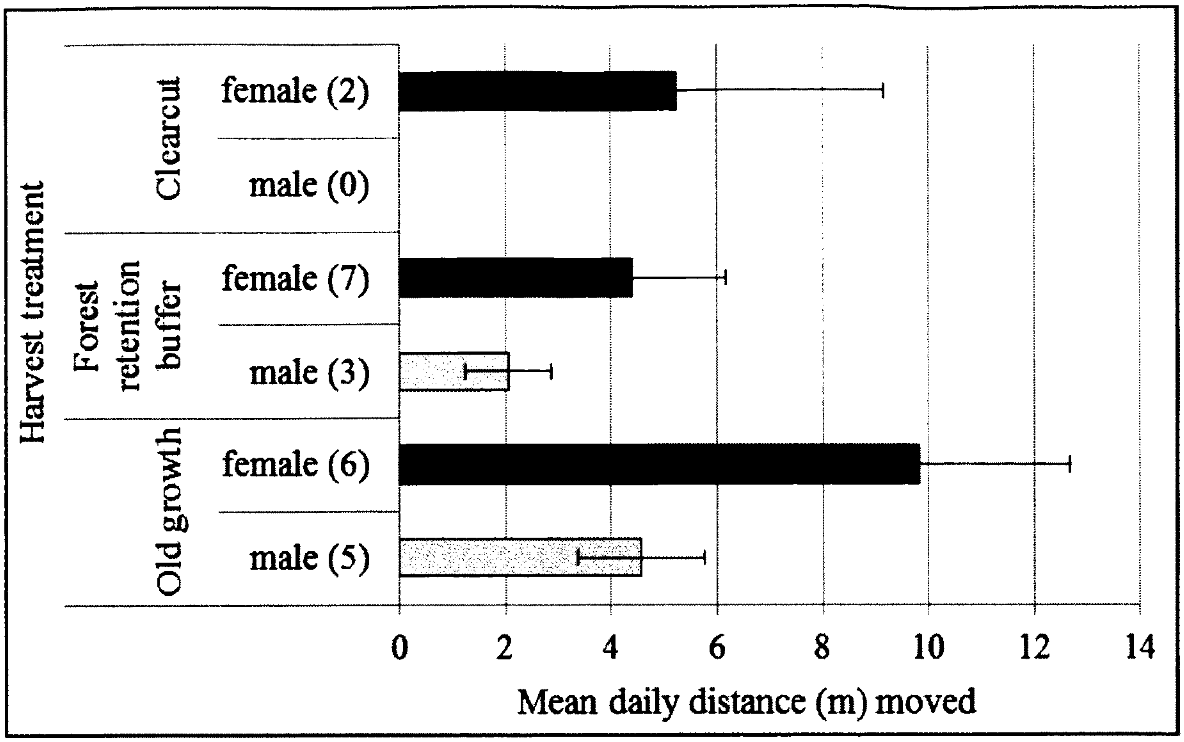

Figure 13. Comparison of the mean daily distance (meters) moved (95% confidence intervals) for 24 adult tailed frogs relocated in 3 forest retention treatments (old growth, forest retention buffer, and clearcut) for 3 watersheds east of Terrace, BC, in 2011 and 2012. Numbers in brackets indicate total number (n) of frogs relocated within each forest retention treatment.

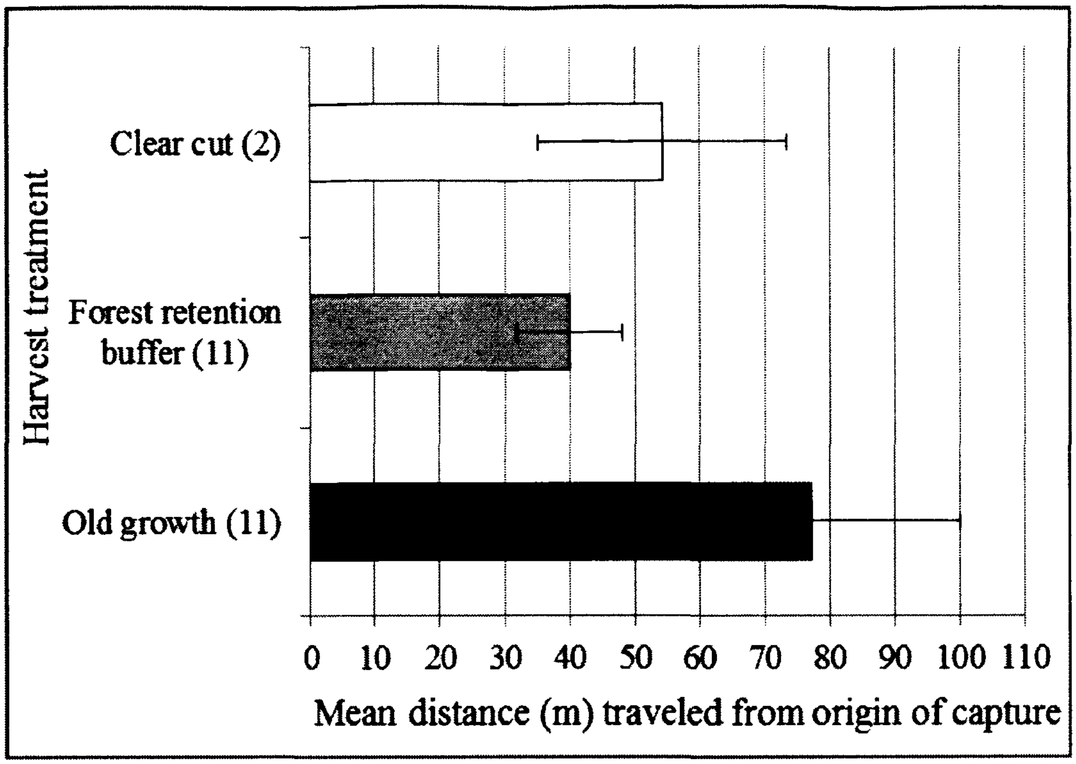

Figure 14: Comparison of the mean distance (meters) traveled from the origin of capture (95% confidence intervals) for 24 adult tailed frogs relocated in 3 forest retention treatments (old growth, forest retention buffer and clearcut) for 3 watersheds east of Terrace, BC, in 2011 and 2012. Numbers in brackets indicate total number (n) of tailed frogs relocated within each forest retention treatment.

The total mean distance traveled from the stream edge decreased in relation to forest harvest and removal of canopy (Figure 15). In the clearcut, the relocations of tailed frogs were on average 2.15 m (SE = 0.55) from the stream edge. However, only two female frogs were monitored in this treatment type. In contrast, female tailed frogs in the forest retention buffer (n = 8) and old growth (n = 6) treatments moved further from the stream edge (27.37 m, SE = 1.72; 64.14 m, SE = 5.11, respectively). Conversely, males had similar movement patterns in relation to the stream for the forest retention buffer (n = 3) and old growth (n = 4) treatments (37.58 m, SE = 1.19; 36.88 m, SE = 3.26, respectively).

As overstory was reduced, tailed frogs had a greater proportion of relocations associated with wet site types. In the old growth treatments, 53.9% of the used locations were in the dry site types. Whereas in the clearcut, 33.33% of the relocations were associated with the wet site type compared to only 14.81% of relocations being associated with the dry site types (Table 9). Females appeared to have greater sensitivity to site moisture when canopy overstory was reduced. Females in the old growth were relocated in the drier site types more often (84.4%) than in the wetter site types (15.6 %;).

Temporal movement

Female tailed frogs generally moved further in the spring (8.32 m, SE = 1.34) while males had greater mean daily movements in the summer (4.49 m, SE = 0.60; Table 10). Although there was no statistical difference in mean daily movements between seasons; in the old growth sites, the greatest mean daily movements occurred during the spring and summer. Conversely, the clearcut treatments had the greatest mean daily movements during the fall although those measures were highly variable and were restricted along the stream edge (Table 11).

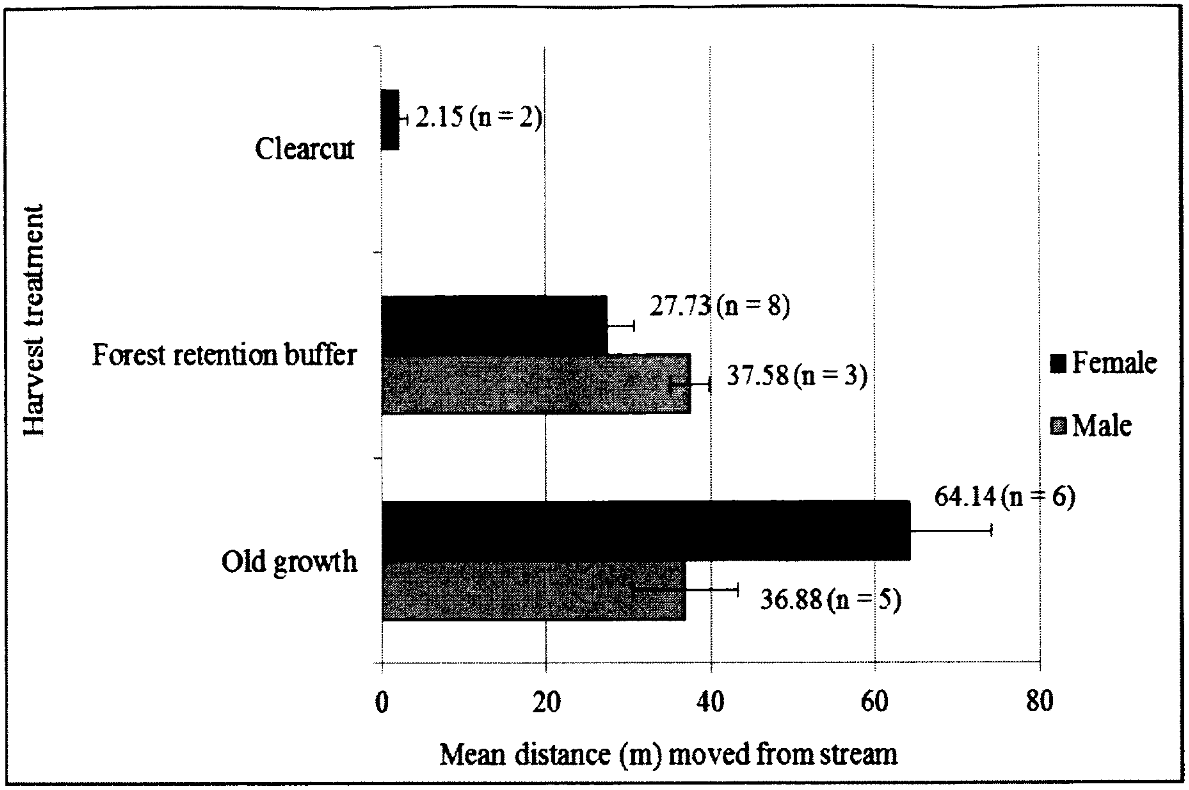

Figure 15: Mean distance (m) moved (95% confidence intervals) from the stream edge for 24 adult tailed frogs relocated in 3 forest retention treatments (old growth, forest retention buffer, and clearcut) for 3 watersheds located east of Terrace, BC, during 2011 and 2012.

Table 9: Radio telemetry data for 24 adult tailed frogs representing the proportions of relocations associated with 4 site moisture types (dry, mesic, subhygric or hygric) for each gender located in 3 forest retention types (old growth, forest retention buffer, and clearcut) for 3 watersheds east of Terrace, BC, during 2011 and 2012. Numbers in brackets represent sample sizes.

Forest retention treatment	**Dry**		**Mesic**		**Subhygric**		**Hygric**	
	Female	**Male**	**Fermale**	**Male**	**Female**	**Male**	**Female**	**Male**
Old growth (128)	33.8 (23)	35.9 (46)	47.1 (32)	5.5 (7)	11.8 (8)	3.9 (5)	3.9 (5)	1.6 (2)
Forest retention buffer (134)	24.6 (33)	19.4 (26)	11.9 (16)	N/A	14.9 (20)	5.2 (7)	17.2 (23)	6.7 (9)
Clearcut (27)	14.8 (4)	N/A	29.6 (8)	N/A	22.2 (6)	N/A	33.3 (9)	N/A

Table 10. Mean distance traveled (m) per day for 24 adult tailed frogs relocated during 2011 and 2012 in 3 watersheds east of Terrace, BC, within 3 forest retention treatments (old growth, forest retention and clearcut). Numbers in brackets represent standard errors (SE).

Gender	Spring	Summer	Fall
Female	8.32 (1.34; n =5)	7.09 (1.44; n = 5)	3.74 (1.27; n = 6)
Male	3.20 (0.52; n = 7)	4.49 (0.60; n = 5)	0.17 (0.08; n = 1)

Table 11: Seasonal daily movement rates for 24 adult tailed frogs located in 3 forest retention treatments (old growth, forest retention buffer and clearcut) for 3 watersheds east of Terrace, BC, during 2011 and 2012. Dates associated with season are located in Table 2. Numbers in brackets represent standard errors and sample sizes (n).

Forest retention treatment	Spring		Summer		Fall	
	Female	Male	Female	Male	Female	Male
Old growth	9.56 (1.78, n = 3)	3.1 (0.73; n = 1)	11.65 (2.5; n = 3)	5 (0.74; n = 1)	N/A	N/A
Forest retention buffer	6.2 (1.92; n = 2)	3.32 (0.79; n = 1)	6.76 (2.08; n = 1)	2.93 (0.74; n = 1)	2.82 (1.08; n = 5)	0.17 (0.08; n = 1)
Clearcut	N/A	N/A	3.44 (0.88; n = 1)	N/A	7.5 (4.45; n = 1)	N/A

Resource selection

When considering the location data for male and female tailed frogs combined, two logistic regression models were responsible for the majority of the AIC_c weight (Table 12). Although, there were nearly twice as many relocations for female frogs, thus, that gender had a disproportionate effect on model selection. The highest ranked model (light + temp2 + moisture + distance to stream + dc2 + dc3 + densiometer) for the pooled location data contained treatment and environmental variables. The second highest ranked model (light + temp2 + moisture + distance to stream + dc2 + dc3) was slightly more parsimonious as it did not include a covariate for canopy closure. This model was selected as the 'best' of the set, but the ROC score suggested 'poor' to 'good' (considering statistical uncertainty) predictive performance (AUC = 0.696, SE = 0.022).

The relocation data for females resulted in 5 logistic regression models representing > 95% of the AIC_c weight. The top ranked model contained a combination of environmental and treatment variables (light + temp2 + moisture + distance to stream + dc3). However, the second ranked model (light + temp2 + moisture + distance to stream) had fewer parameters ($k = 8$) and was therefore selected as the 'best' of the model sets. The ROC score for this model suggested 'good' predictive performance (0.734, SE = 0.027). For male tailed frogs, > 95% of the AIC_c weight was represented by 5 models. The top ranked model consisted of only treatment variables (distance to stream + dc1 + dc2 + dc3; Table 13). Resource selection models generated for male tailed frogs had consistently 'poor' predictive performance (AUC < 0.676).

Table 12: Most parsimonious logistic regression models (AIC_c) for relocation data of 24 tailed frogs in 3 watersheds east of Terrace, BC, in 2011 and 2012. Top ranked models represented $\geq$ 95% of the AIC_c weight ($\text{AIC}_c\ w$); the area under the curve (AUC, Standard Error) represents the measure of predictability for each model.

Model	Rank	*k*	AIC_c	ΔAIC_c	$\text{AIC}_c\ w$	AUC (SE)
Female and Male						
light+temp2+distance to stream+dc2+dc3+densiometer+moisture*	1	11	274.381	0.0	0.573	0.706 (0.022)
light+temp2+distance to stream+dc2+dc3+ moisture*†	2	10	275.001	0.6	0.420	0.696 (0.022)
Female						
light+temp2+distance to stream +dc3+moisture*	1	9	134.860	0.0	0.389	0.764 (0.025)
light+temp2+distance to stream +moisture*†	2	8	135.409	0.5	0.294	0.734 (0.027)
light+temp2+distance to stream+dc2+dc3+ moisture*	3	10	137.353	2.5	0.111	0.772 (0.025)
light+temp2+distance to stream+dc3+densiometer+ moisture*	4	10	137.590	2.7	0.099	0.765 (0.025)
light+temp2+distance to stream+densiometer+ moisture*	5	9	137.940	3.1	0.083	0.736 (0.026)
Male						
dc1+dc2+dc3+distance to stream†	1	4	103.702	0.0	0.401	0.655 (0.039)
dc1+dc2+dc3+distance to stream+light	2	5	104.150	0.4	0.321	0.663 (0.039)
dc1+dc2+dc3	3	3	106.448	2.7	0.102	0.676 (0.038)
dc1+dc2+dc3+light+temp2+ distance to stream*	4	7	107.001	3.3	0.077	0.630 (0.040)
dc1+dc2+dc3+distance to stream+temp2 +densiometer*	5	6	107.786	4.1	0.052	0.635 (0.040)

*Both the linear and quadratic terms were applied to model.

†Most parsimonious model identifying forest attributes post-metamorphic tailed frogs use.

Table 13: Coefficients and measure of statistical significance, including 95% confidence intervals (CI), for covariates from the most parsimonious logistic regression models (Table 13) generated using relocation data for tailed frogs collected in 2011 and 2012 from 3 watersheds east of Terrace, BC.

Variable	Coefficient	SE	z	*p*	Lower 95% CI	Upper 95% CI
Female and Male						
light	-0.001	0.001	-1.71	0.087	-0.002	< 0.001
temp	0.878	0.377	2.33	0.02	0.140	1.617
temp2	-0.029	0.016	-1.87	0.062	-0.059	0.001
distance to stream	-0.019	0.010	-1.83	0.068	-0.040	0.001
decay class 2	0.001	< 0.001	1.7	0.089	< -0.001	0.001
decay class 3	< 0.001	< 0.001	2.36	0.018	< 0.001	< 0.001
dry	-0.750	0.310	-2.42	0.016	-1.358	-0.142
mesic	-0.146	0.231	-0.63	0.527	-0.599	0.307
subhygric	-0.119	0.242	-0.49	0.623	-0.594	0.356
hygric	1.015	0.498	2.04	0.042	0.039	1.991
Female						
light	-0.003	0.001	-2.91	0.004	-0.005	-0.001
temp	0.208	0.319	0.65	0.515	-0.417	0.833
temp2	0.008	0.020	0.42	0.671	-0.030	0.047
distance to stream	-0.013	0.017	-0.75	0.454	-0.046	0.020
dry	-1.195	0.440	-2.71	0.007	-2.057	-0.332
mesic	-0.333	0.291	-1.14	0.253	-0.904	0.238
subhygric	0.011	0.275	0.04	0.967	-0.527	0.550
hygric	1.516	0.691	2.19	0.028	0.161	2.871
Male						
distance to stream	-0.034	0.013	-2.57	0.010	-0.061	-0.008
decay class 1	0.001	0.001	1.49	0.135	< -0.001	0.002
decay class 2	0.003	0.001	2.80	0.005	0.001	0.004
decay class 3	< 0.001	< 0.001	0.16	0.812	< -0.001	< 0.001

Adult tailed frogs were significantly associated with non-vascular and shrubby vegetation found in the wetter site types and with coarse woody debris in decay classes > 2 ($p < 0.05$; Table 14). The distribution of tailed frogs was negatively associated with decreasing canopy closure, increasing light, sites containing drier vegetation, and an increased distance from the stream; however, only drier site types were statistically significant ($p < 0.05$). Furthermore, the nonlinear temperature term (linear and quadratic) was positively associated with tailed frog presences in the model using the pooled data up to 11°C after which the probability of a tailed frog using a location decreased (Appendix VI).

Females used locations with temperatures of approximately 11°C and demonstrated a strong negative association with increasing light and a drier moisture regime, while having a greater association with wetter site types ($p < 0.05$). Males used locations with temperatures of approximately 12°C, were negatively associated with an increasing distance from the stream edge, and positively associated with coarse woody debris, principally decay class 2 ($p < 0.05$; Table 14).

DISCUSSION

Currently, there is little information describing the movement patterns and habitat requirements of tailed frogs in the terrestrial environment. Previous studies have used pitfall trapping and visual encounter surveys (Maxcy 2000; Wahbe *et al.* 2004; Matsuda and Richardson 2005; Hayes *et al.* 2006; Burkholder and Diller 2007). These techniques have limited utility for describing the fine-scale movements, patterns of resource use or distribution of the species as the recapture rate of individual tailed frogs can be low (Wahbe *et al.* 2004; Matsuda and Richardson 2005; McEwan Unpub. Data). A better understanding of the terrestrial habitat requirements of the tailed frog is essential if conservation and management activities are to be effective.

Researchers have quantified the average movement rates for populations of tailed frogs in southern BC within seasons (e.g., 3.0 m/day in the fall; Wahbe *et al.* 2004) and relative to habitat alterations (e.g., average daily movement rate of 12.27 m, SE = 3.48 in forested stands compared to 8.53 m, SE = 5.01 in buffered stands; Maxcy 2000). The average minimum distance traveled within fixed pitfall grids in southern BC populations has been estimated as 42.86 m (SE = 6.96; Maxcy 2000).

The patterns of movement within my study are representative of daytime activity of a nocturnal species. However, this study increases our knowledge on the movement between potential daytime refugia; particularly when climatic conditions are not favorable (increased temperature and decreased moisture). This population in northwestern BC, had a mean daily distance traveled of 5.49 m/day (SE = 0.53), with some individuals traveling up to 45 m between daily relocations.

Gender differences in movement

Understanding movement rates reflective of the biological demands of each gender can assist with the conservation of the species. For example, Hayes *et al.* (2006) suggested that female tailed frogs undergo movements to productive headwaters after ovipositioning, likely to acquire food resources for future yolk production. In my study, 9 females had a total distance traveled > 40 m and had greater estimated space use than males. However, the distances that females traveled were highly variable suggesting a considerable range of seasonal ecological (reproduction) or physiological (thermal- and hydric-regulatory) demands. Conversely, 5 males had a total distance traveled < 40 m implying a greater philopatry to particular areas, although the mechanisms for this behavior are unclear. Similar patterns in movement by male and female *A. truei* were observed by Burkholder and Diller (2007) in northwestern California, where females underwent greater parallel movements within the stream compared to both adult and immature males.

Forest retention treatment and movement of tailed frogs

Previous research has suggested that timber harvest is a barrier to amphibian movement restricting dispersal and reducing migration (Johnston and Frid 2002; Matsuda and Richardson 2005; Baldwin *et al.* 2006; Hawkes and Gregory 2012). Forest harvesting reduces or eliminates canopy overstory, altering the microclimate at the forest floor, including the availability of moist microsites that can act as thermal- and hydric-refugia (Corn and Bury 1991; deMaynadier and Hunter 1999; Brosofske *et al.* 1997; Johnston 1998). Tailed frogs are known to be sensitive to local environmental changes because of their ectothermic nature and fidelity to breeding locations (Daugherty and Sheldon 1982; Nussbaum *et al.* 1983; Wahbe *et al.* 2004; Matsuda and Richardson 2005; McEwan Pers. Obs.).

The movement and habitat selection of female frogs reflected the interaction between the ecology and physiology of the species with the history of forest harvesting at each site. For example, females in the old growth traveled further from the stream suggesting that the overstory and on-ground structural complexity created appropriate habitat conditions relative to the thermo- and hydro-regulatory requirements of the species. Likewise, as overstory was reduced, the distance traveled from the stream decreased and movement became more parallel with the stream (Figure 15). These differences in movement suggest that physical constraints (increased temperature and decreased moisture) limited perpendicular movement.

Thus, the riparian area close to the stream and moist microsites within a site may act as habitat refugia facilitating upstream/downstream movement and ameliorate the dry conditions found across the broader clearcut matrix.

Temporal distribution

Previous research has proposed that *A. truei* undergo migration to facilitate reproduction or to accommodate changing environmental conditions (Landreth and Ferguson 1967; Brown 1975; Wahbe *et al.* 2004; Hayes *et al.* 2006). Wahbe *et al.* (2004) suggested that *A. truei* males in southwestern BC traveled upstream to locate mature females during the breeding season and gravid females moved towards the stream for ovipositioning; although, there is little direct evidence relating movement to reproduction. *A. montanus* is known to move downstream during the fall in response to decreasing water temperatures (Adams and Frissell 2001).

Pre-oviposited females were located moving towards the stream (Chapter 2). After eggs were deposited under rocks or debris within the larval streams (Karracker *et al.* 2006), females moved away from the larval stream (Chapter 2). During this time, females had the greatest daily movements (8.32 m, SE = 1.34). With the onset of cooler temperatures and increased precipitation in the fall, females were seen in old stream channels containing moving water where breeding was occurring (McEwan Pers. Obs.). During this time, daily movements decreased (3.73 m SE = 1.27). These movement patterns suggest that female tailed frogs may express migratory behaviour in response to annual or biennial reproductive events.

Conversely, I did not observe large movements by male tailed frogs. Individuals remained close to the origin of capture with the lowest rate of movement occurring during the fall (0.16 m SE = 0.08). Reduced movement within the breeding season has perhaps evolved with the inability of the species to vocally communicate (Schmidt 1970) or is a function of spatially discrete breeding locations (Todd *et al.* Unpub Data). Additionally, tailed frogs fitted with transmitters became subterranean in the late fall and remained there until the transmitter signal stopped. This may suggest that over-wintering occurs in the same vicinity as the breeding locations.

Statistical models identifying habitat use by tailed frogs

Understanding habitat use at multiple scales is essential if we are to consider the full range of habitat requirements for species of concern like the tailed frog. Distributional choices an individual makes at a broad scale can influence or interact with behaviours, including habitat use, at a finer level (Rettie and Messier 2000). For example, the thermo- and hydro-regulatory demands of amphibians suggests that the use of habitat at the coarse scale, such as forest retention treatment, is mechanistically linked to finer-scale use of individual habitat features including wet micro-sites or CWD (Blomquist and Hunter 2010).

With the miniaturization of radio-telemetry devices, the application of species distribution models to data for small (< 10 g) herpetofauna has become more common. For example, Faccio (2003) used radio-telemetry to quantify the habitat and area used by *Ambystoma* salamanders (*A. maculatum* and *A. jeffersoniaum*) near breeding ponds. Blomquist and Hunter (2010) used radio-telemetry data for wood frogs to study fine-scale habitat selection across 4 timber forest retention treatments in Maine. My study, however, is the first to use radio-telemetry to quantify resource selection and movement of *Ascaphus* spp. Also, I considered resource selection relative to habitat features and site conditions that were measured at two spatial scales across a 4-month growing season.

Previous work suggests that CWD is an important structural component for maintaining amphibian diversity in forested stands of the Pacific Northwest (reviewed by deMaynadier and Hunter 1995). This forest attribute provides shelter, protection from predation and ameliorates the thermo- and hydro-regulatory limits of these taxa (Corn and Bury 1991; Petranka *et al.* 1994; deMaynadier and Hunter 1995; Butts and McComb 2000; Bull 2002; Faccio 2003; Kluber *et al.* 2008; Blomquist and Hunter 2010). Older decay classes are typical in mature stands (Spies and Cline 1988) and are known to have greater water holding capabilities (Jager 1980). In addition, downed wood contains high proportions of invertebrates (Harmon *et al.* 1986; Lockaby *et al.* 2002) and amphibians forage in and around CWD (Loeb1999; Whiles and Grubaugh 1996).

The RSF models identified a significant association between the location of tailed frogs and CWD in older decay classes (i.e., decay classes 2 and 3; Table 14). This relationship was strongest for male frogs. Male frogs also demonstrated greater site fidelity and limited dispersal, as indicated by decreased movement (< 40 m) from the origin of capture. Coarse woody debris would provide shelter and a microclimate required by the tailed frog (low temperature and increased moisture) thereby reducing movement.

Although CWD can increase at a site following forest harvesting (Harmon *et al.* 1996), Spies and Cline (1988) suggest that this newly added CWD is often not decayed and smaller in diameter with less volume, which reduces its ability to hold water. A relatively small sample of monitored tailed frogs within the clearcut treatments limits our understanding of the resources used within those stands. However, the positive association with CWD in upper decay classes suggests that this habitat feature is a valuable resource for tailed frogs.

The RSF models identified a positive association between the locations of tailed frogs and wetter site types, indicated by lady fern, devil's club and leafy mosses. These wet site types would meet the physical and ecological demands of tailed frogs and facilitate movement from stream edge, especially in sites where timber harvest has resulted in increased temperatures and decreased moisture. For example, females relocated in the clearcut, had a greater proportion (55.5%) of their relocations in either subhygric or hygric site types (Table 8).

When compared to random locations, male tailed frogs had greater association with locations near the stream (< 40 m). This may have been reflective of their origin of capture and limited movement (36.85 m, SE = 7.87) during the monitoring period. However, populations of *A. truei* in southern (Wahbe *et al.* 2004; Matsuda and Richardson 2005) and northwestern BC (Chapter 2) also used habitats adjacent to the maternal stream. Tailed frogs are more prone to desiccation than other anurans (Claussen 1973a), thus, habitats adjacent to or within riparian areas may provide wet and cool microclimates (Brosofske *et al.* 1997; Chen *et al.* 1999).

Temperature is critically important for the timing of emergence, breeding, embryological development and growth of amphibians (Brattstrom 1963). Previous works have demonstrated that *Ascaphus* have ambient air temperature thresholds between 24-27.6˚C. For example, Brown (1975) reported that *A. montanus* has a maximum temperature tolerance of 24˚C; Claussen (1973a) reported that populations of *A. truei* along their southern range have critical thermal maxima of 27.6°C; and *A. truei* in northwestern BC were not found in traps when ambient air temperatures were > 26.5°C (McEwan Unpub. Data).

However, many studies use air temperatures that reflect the macro-environment not temperatures associated with the micro-habitat selected by frogs.

Removal of forest cover at ≥ 17 m from the stream can result in temperature increases of 2-4°C and a decrease in relative humidity of 2.5-13.8% (Chen *et al.* 1999). Within this study, the most parsimonious model suggested tailed frogs used locations with temperatures between 11-12°C (Appendix VI); however, tailed frogs were found at locations with temperatures up to 24°C. Furthermore, the 2 females relocated in the clearcut treatments were on average monitored close to the stream (2.15 m, SE = 0.55) and used locations with understory vegetation representative of wetter site types (Table 9) that would provide thermal and hydric refugia.

Removal of overstory increases the penetration of light to the forest floor thereby altering the microclimate and vegetative structure (Greenberg 2001). Even with partial canopy removal, an increase in light can adversely affect amphibian abundance (deMaynadier and Hunter 1995, 1999). For example, Knapp *et al.* (2003) reported that > 41% of canopy removal resulted in declines of populations of plethodontid salamanders in the southern Appalachians. Likewise, Baldwin *et al.* (2006) reported that during post-breeding migration wood frogs selected locations that were dark, moist and had closed canopies. The RSF model for the female data identified a negative association with increasing light levels ($p < 0.01$). Similarly, I observed female tailed frogs using microhabitats with low levels of light: only 9.2% of used locations had light levels > 10^3 lux, comparable to an overcast day (Appendix VII). Use of habitats with lower light may be an artifact of the species' nocturnal behaviour (Metter 1967; Bury 1970), especially as monitored frogs were relocated during the day. However, the use of locations with lower ambient light could also indicate a relationship between canopy closure and its influence on the microclimate and the use of certain forest attributes like CWD. Both variables were included in the top RSF models (Table 14).

CONCLUSION

I tested 3 main predictions based on existing knowledge of forest-dependent amphibians like the tailed frog. Previous studies have reported the positive association of amphibians with forest features such as CWD that ameliorate site conditions by providing shelter and increasing the availability of food resources. Within the scope of my study, adult tailed frogs demonstrated a positive association with CWD of the oldest decay classes. Second, I predicted that during the warmer and drier portions of the year, tailed frogs would be located close to the stream and with habitat features that reduced thermal stress. Although tailed frogs were located closer to the stream in the summer compared to the spring, the greatest adjacency occurred during the fall. This suggests that the breeding phenology of the species is a strong driver of seasonal distribution. Additionally, tailed frogs were associated with locations with temperatures of 11°C as seen in the RSF model. Lastly, I predicted that as overstory declined *A. truei* would have a greater association with habitat features that ameliorate dry or warm stand conditions. Adult tailed frogs had a significant association with wet microsites and avoided drier types; this was especially true in the clearcut treatments.

RECOMMENDATIONS

Forest management and the tailed frog

Forest management practices can directly affect the integrity of habitat required by the tailed frog at a number of ecological and evolutionary scales. Our understanding of the ecology of semi-aquatic species, like the tailed frog, is often focused on the larval stage or near-stream locations of the post-metamorphs. This is in part reflective of the species' cryptic and fossorial nature. Thus, we have a limited understanding of the use and importance of upslope habitats where tailed frogs spend the majority of their life. Documenting the species' movement and distribution at multiple scales, including habitat use across fragmented landscapes, is necessary for maintaining important forest features, stand conditions, and habitat connectivity that facilitates long-term gene flow among populations.

Tailed frogs in northwestern BC demonstrated a positive association with moist or wet microhabitats, as indicated by vegetation type and CWD in the older decay classes. These habitat features likely ameliorate extremes in temperature allowing tailed frogs to meet thermal- and hydro-regulatory limits. Additionally, tailed frogs used locations with cooler temperatures (11-12°C) that were well below the thermal tolerance of the species (24°C; Brown 1975). However, the structure of the best RSF model did vary when considering locations separately for male and female tailed frogs. Females used locations with low light levels ($< 10^3$ lux) and avoided drier site types, while males remained in locations close to a stream (< 40 m) with moderately decomposed CWD (decay class 2). Furthermore, assessments of the predictive capacity of each set of models suggested that females were more selective in their choice of habitat (i.e., greater AUC).

These results confirm past work that has related the ecological requirements of tailed frogs to thermal and hydric limits (Metter 1967; Brown 1975; Daughtery and Sheldon 1982) and recommended that land management practices retain intact overstory and complex forest structure (Wahbe *et al.* 2004; Matsuda and Richardson 2005). For example, Spears and Strofer (2008) found that certain landscape features, such as forest cover, had a strong influence on the population structure of tailed frogs. A reduction in the overstory canopy creates fragmented habitats ultimately limiting dispersal and gene flow among and potentially within populations. Hawkes and Gregory (2012) documented a time lag in the response by tailed frogs to overstory removal such that the number of individuals decreased 10-years post-harvest compared to pre-harvest numbers.

Previous studies reported a positive association between the distribution of tailed frogs and specific forest attributes including CWD, decreased light intensity, and moist microsites that ameliorate site conditions after a disturbance. For example, Butts and McComb (2000) suggested that the retention of CWD in managed stands closely mimic those volumes found in natural stands (248 m^3/ha) in the western Cascades of Washington. Baldwin *et al.* (2006), Rittenhouse and Semlitsch (2008), and Blomquist and Hunter (2010) all speak to the importance of preserving forest attributes, including CWD and moist microsites that create thermal- and hydric-refugia. These refugia can facilitate movement across landscapes fragmented by anthropogenic disturbances such as timber harvest.

Consistent with past studies, my findings suggest that conservation planners should consider fine-scale habitat features when designing reserves (e.g., Wildlife Habitat Areas) and managing forest harvest to conserve populations of the tailed frog. First, the most effective, but costly strategy is to maintain old forest types that provide suitable climatic and structural conditions required by tailed frogs (i.e., moist microsites, CWD in decay classes $\geq$ 2 and temperatures between 11-12°C). These habitat conditions are essential for maintaining individual populations of tailed frog and will facilitate movement by the reproductive core of the population (i.e., females). Second, across managed forests, strategies should be designed to preserve important microsites and habitat features, such as wet drainages and CWD that provide thermo- and hydro-regulatory refugia. Third, where harvesting occurs, a wind-firm forest retention buffer should be maintained around maternal streams. This buffer should be of sufficient size to ameliorate changes in the understory microclimate resulting from adjacent forest harvesting. These buffers will maintain essential reproductive and rearing habitats and facilitate seasonal migration and population connectivity (Spears and Strofer 2008). By maintaining functional habitat for the tailed frog across forest patches and landscapes, we can conserve this species at their northern range limit, including the maintenance of evolutionary processes.

CHAPTER 4

GENERAL SUMMARY

There have been relatively few studies on the biology or ecology of the post-metamorphic coastal tailed frog, especially at the northern distribution of the species. Hence, the majority of our knowledge is attributed to interior and southern populations of *Ascaphus* with a particular focus on the larval life stage (Daugherty and Sheldon 1982; Bury and Adams 1999; Dupuis and Steventon 1999; Maxcy 2000; Wahbe and Bunnell 2001; Wahbe *et al.* 2004; Matsuda and Richardson 2005; Hayes *et al.* 2006; Karracker *et al.* 2006; Burkholder and Diller 2007). I used an Information Theoretic Model Comparison approach to quantify the distribution, movement patterns, and resource selection of post-metamorphic coastal tailed frog (*A. truei*). For *A. truei* in northwestern BC, this study was the first to: 1) describe the movement and fine-scale distribution of the post-metamorphic tailed frog in response to ecological, biological and disturbance factors; and 2) create resource selection functions identifying the fine-scale habitat requirements of the species. Although this study is relevant to populations of *A. truei* in northwestern BC, the use of these techniques can be applied to populations of *Ascaphus* throughout their range. A better understanding of the distribution, movements, and resource selection of this species can assist with conservation actions and the mitigation of impacts from anthropogenic disturbances including timber harvest, independent power projects and linear features such as oil and gas pipelines.

In Chapter 2, I used 2 consecutive years of capture data to quantify the movement patterns and relative abundance of post-metamorphic tailed frogs across terrestrial habitats within two watersheds. The fine-scale distribution of tailed frogs was systematically monitored using pitfall traps installed at 4 forest retention treatments. Emergence from over-wintering sites and movement by females for ovipositioning appeared to correspond with warmer temperatures and melting of the snow pack. Furthermore, direction of movement was specific to time of year and the reproductive status or gender of the tailed frog. Juveniles are known dispersers (Daughtery and Sheldon 1982) and were documented moving away from the stream in the old growth and clearcut treatments, females moved away from the stream after ovipositioning, and newly metamorphosed frogs were located moving upstream after emergence. The majority of captures were in the 5 m arrays, associated with rain events (< 1 day) and during the months associated with the breeding phenology of the species. Furthermore, canopy cover influenced movement and capture rate as the number of frogs caught per unit effort decreased as the overstory canopy was reduced following forest treatment. This was particularly evident with the large sample size from the 2012 trap year. These results are consistent with past research in other regions that noted a relationship between the distribution and activity of tailed frogs relative to micro-site and broader climatic conditions as influenced by forest overstory and structural complexity (Daughtery and Sheldon 1982; Aubry 2000; Matsuda and Richardson 2005).

Temporal variation in capture success suggests that the pitfall trap method and resulting data are influenced by season, likely mediated by climate trends, and the reproductive biology and resulting behaviour of tailed frogs. Thus, the timing and extent of trap sessions can greatly influence capture results and the observed movements of frogs, at least at the northern extent of their range. These findings are useful when designing inventory protocols for *A. truei*, specifically: 1) the time of year to conduct surveys designed to monitor fine-scale distribution and detect the presence of post-metamorphic tailed frogs within a stream reach or watershed; and, 2) the proximity of searches to a stream (≤ 50 m) either for the placement of pitfall traps or areas to focus visual encounter surveys.

In Chapter 3, I used radio-telemetry data to quantify the resource selection of adult *A. truei* across forest retention treatments. These results allowed me to identify the features and the micro-scale attributes of habitat likely important to the thermo- and hydro-regulatory processes of *A. truei*. In general, adult tailed frogs used locations that afforded the greatest protection from desiccation (increased moisture) and were characterized by decayed coarse woody debris, low light, and cool temperatures (11-12°C). However, movement patterns and habitat use differed between female and male tailed frogs. Females moved greater distances and were more sensitive to temperature and moisture constraints. In addition, females made large-scale movements associated with the reproductive phenology of the species. Conversely, male frogs demonstrated greater philopatry to a location (< 40 m from origin of capture), remained close to the stream (< 40 m) and increased their daily movement during the summer compared to the spring (1.4 times greater). Such movements were likely associated with foraging or to access habitat that provided protection from physical constraints (increased temperature and decreased moisture).

Through this study I documented or inferred seasonal movement patterns at a range of ecological scales and I identified the habitat requirements, including micro- and macro-scale features that were related to the ecological and physical requirements of *A. truei* found at the northern extent of its range. For instance, female movements coincided with reproductive needs such as ovipositioning (spring) and breeding (fall). Additionally, tailed frogs were seen using breeding locations annually and these sites have the potential to be important over-wintering habitat. Furthermore, the observed movement patterns and fine-scale distribution revealed the dependency of this species to the near-stream environment, especially when canopy cover was reduced creating warmer and drier stand conditions.

Finally, the biological and physical requirements of this species, in addition to observed habitat use and fine-scale distribution, suggested that the most appropriate forest types had mature standing timber with complex structure in the understory, specifically cool, moist microsites and CWD in decay classes ≥ 3.

Conservation Recommendations

Findings from this study, in combination with conservation theory and current understanding of *A. truei*, can be used by land managers to identify appropriate habitat reserves (e.g., Wildlife Habitat Areas) and may assist with the design of movement corridors across landscapes. Such a conservation network would be composed of riparian reserve zones, riparian management zones and linkages to adjacent watersheds. Of greatest priority, habitat should be conserved near the larval stream. These areas support all life stages of *A. truei* and are essential for reproduction and ultimately population persistence and dispersal. To protect the intact overstory and structural complexity of the understory near these areas, a Riparian Reserve Zone should be placed on both sides of the larval stream (Chen *et al.* 1999), specifically along stream reaches where ovipositioning occurs. In addition to being the source of juvenile frogs, these areas have high densities of adult frogs during periods of the year associated with reproduction.

Data from this study revealed that post-metamorphic tailed frogs are found at distances beyond the 30-50 m buffers currently proposed for habitat reserves (BCMWLAP 2004). However, to fully quantify the buffer width in riparian areas, more work is required to assess long-term movement. Such a study would require multiple successive transmitters placed on individuals allowing for the measurement of movement dynamics that exceed the shorter period of monitoring (mean = 10.75 days, SE = 0.89) applied to this research. Such data would better quantify the distance traveled by females seasonally thereby increasing the certainty of dispersal capabilities of the species.

Consistent with theory, past work, and the current strategy of habitat reserves for tailed frogs in BC, I recommend a Riparian Management Zone adjacent to the Riparian Reserve Zone. Forest harvesting would be permitted in this zone, but there would be an emphasis on retaining ground-level forest structure and moist microsites. These habitat features would ensure physical and foraging refugia with temperatures reflective of locations used by tailed frogs (11-12°C) in this study. Similar to past research on amphibians, the tailed frog demonstrated a positive association with CWD specifically in decay classes 3-5 (BC MELP 1998); however, the minimum quantity that should be retained within the Riparian Management Zone requires further investigation.

Riparian Management Zones should follow the current stand retention and best management practices for S5 (non-fish bearing) streams located in valley bottoms: 1) the retention of 50% of the dominant and co-dominant overstory that would reduce the risk of windthrow; 2) retention of non-merchantable timber and herbaceous vegetation within 10 m of the stream channel, 3) ensure that falling and yarding occur away from the stream and remove any slash or debris that enters the stream; and, 4) retention of wildlife trees (BC Ministry of Forests and Ministry of Environment1995). Finally, movement corridors or linkage zones should be created between riparian reserves allowing for genetic dispersal (Beier *et al.* 2008). In southerly populations of *A. truei*, Spear and Strofer (2008) demonstrated genetic similarities among watersheds up to 25-30 km apart. Thus, a study of genetic connectivity for northern populations of the tailed frog will increase our understanding of the importance and proper placement of movement corridors (Murphy *et al.* 2010).

If the aforementioned recommendations are followed, then *A. truei* may persist across a landscape consisting of a patchwork of timber harvest and intact forests connected by movement corridors. Moreover, by creating useable habitat for the tailed frog that retains mature stand attributes and intact corridors between watersheds, other old-forest flora and fauna will benefit. Likewise, retention of intact headwaters that are non-fish bearing and contain *A. truei* also will protect the downstream waters of fish-bearing streams by decreasing sedimentation and temperature fluctuations (BC Ministry of Environment 2004).

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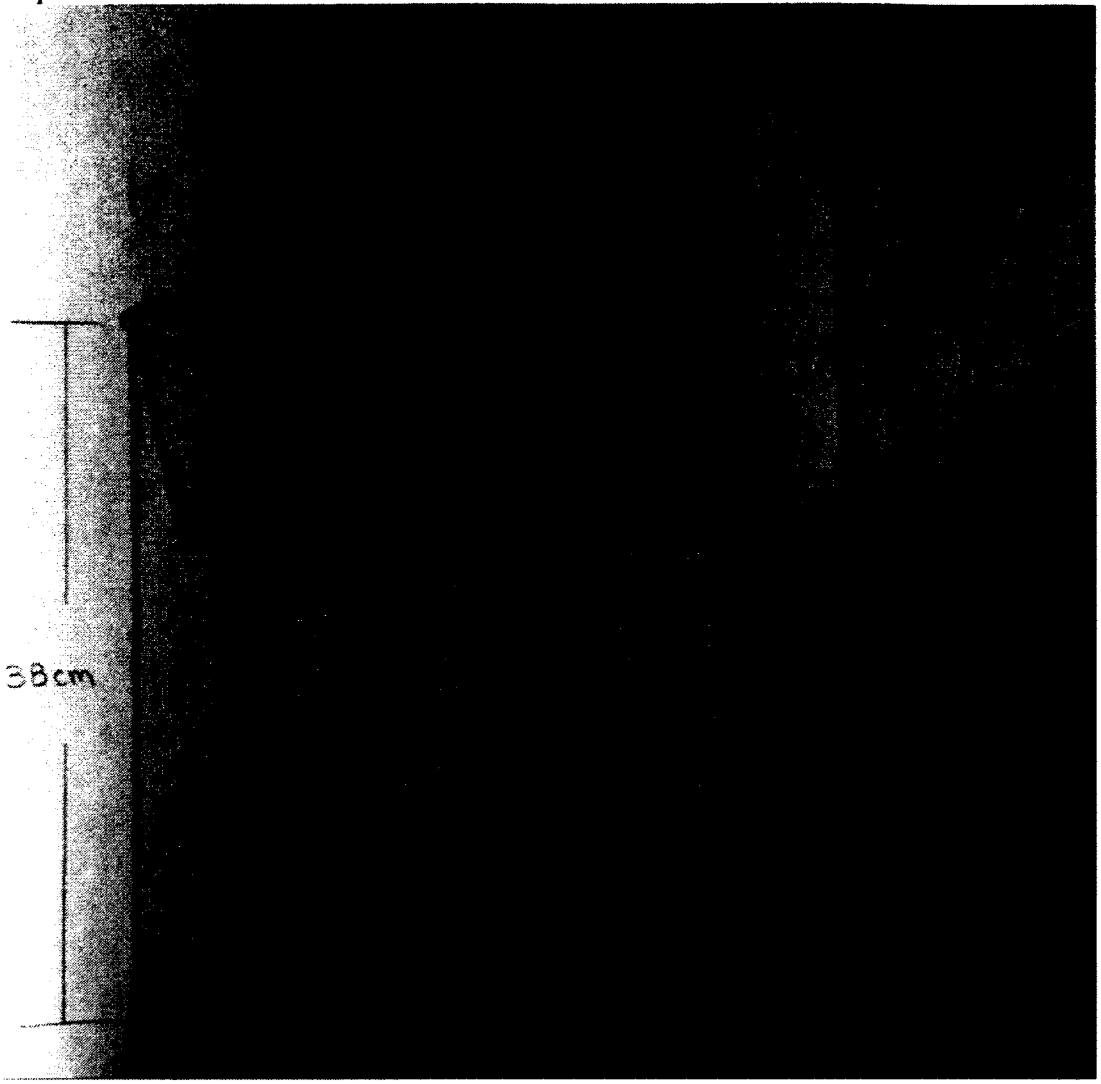
Appendix I- Diagram demonstrating the pitfall trap with plastic insert and escape rope. During the 2012 spring session, the escape rope did not contain knotted sections. After discussion with M. Todd, knotted sections were implemented for the remainder of the 2012 trap session and all of 2013 sessions.



Appendix II- Logistic regression models used for the 2012 trap data conducted in 2 watersheds located east of Terrace, BC, identifying the distribution of tailed frogs within forest retention treatments.

	k	Log Likelihood	-2LL	AIC	AIC$_c$	Δ AIC	AIC weight
TEMPORAL							
trap_month	4	-514.932	1029.865	1037.865	1038.891	85.3	< 0.0001
TREATMENT							
densiometer site_moisture	6	-506.428	1012.856	1024.856	1027.127	73.6	< 0.0001
canopy_code de_transition distance_stream	9	-488.819	977.639	995.639	1000.933	47.4	< 0.0001
distance_stream de_transition	5	-489.436	978.872	988.872	990.450	36.9	< 0.0001
site_moisture distance_stream de_transition	9	-486.976	973.953	991.953	997.247	43.7	< 0.0001
distance_stream	2	-491.792	983.584	987.584	987.877	34.3	< 0.0001
site_moisture	5	-511.260	1022.519	1032.519	1034.098	80.6	< 0.0001
de_transition	4	-508.890	1017.781	1025.781	1026.807	73.3	< 0.0001
canopy_code	5	-510.637	1021.273	1031.273	1032.852	79.3	< 0.0001
site_elevation site_elevation2	3	-506.884	1013.768	1019.768	1020.368	66.8	< 0.0001
site_elevation site_elevation2 distance_stream	4	-481.048	962.096	970.096	971.121	17.6	< 0.0001
densiometer	2	-510.837	1021.674	1025.674	1025.967	72.4	< 0.0001
orientation distance_stream de_transition	9	-485.402	970.803	988.803	994.098	40.6	< 0.0001
ENVIRONMENTAL							
temp_difference hum_difference	3	-504.073	1008.145	1014.145	1014.745	61.2	< 0.0001
temp_difference	2	-507.130	1014.259	1018.259	1018.552	65.0	< 0.0001
temp_min temp_min2	3	-514.469	1028.938	1034.938	1035.538	82.0	< 0.0001
temp_max temp_max2	3	-512.726	1025.453	1031.453	1032.053	78.5	< 0.0001
days_rain	2	-505.395	1010.789	1014.789	1015.082	61.5	< 0.0001
hum_difference	2	-504.106	1008.212	1012.212	1012.505	59.0	< 0.0001
ENVIRONMENTAL & TREATMENT COMBINED							
distance_stream temp_difference	3	-484.228	968.457	974.457	975.057	21.5	< 0.0001
distance_stream hum_difference	3	-482.626	965.252	971.252	971.852	18.3	< 0.0001
de_transition temp_max2 temp_max	6	-506.506	1013.012	1025.012	1027.283	73.7	< 0.0001

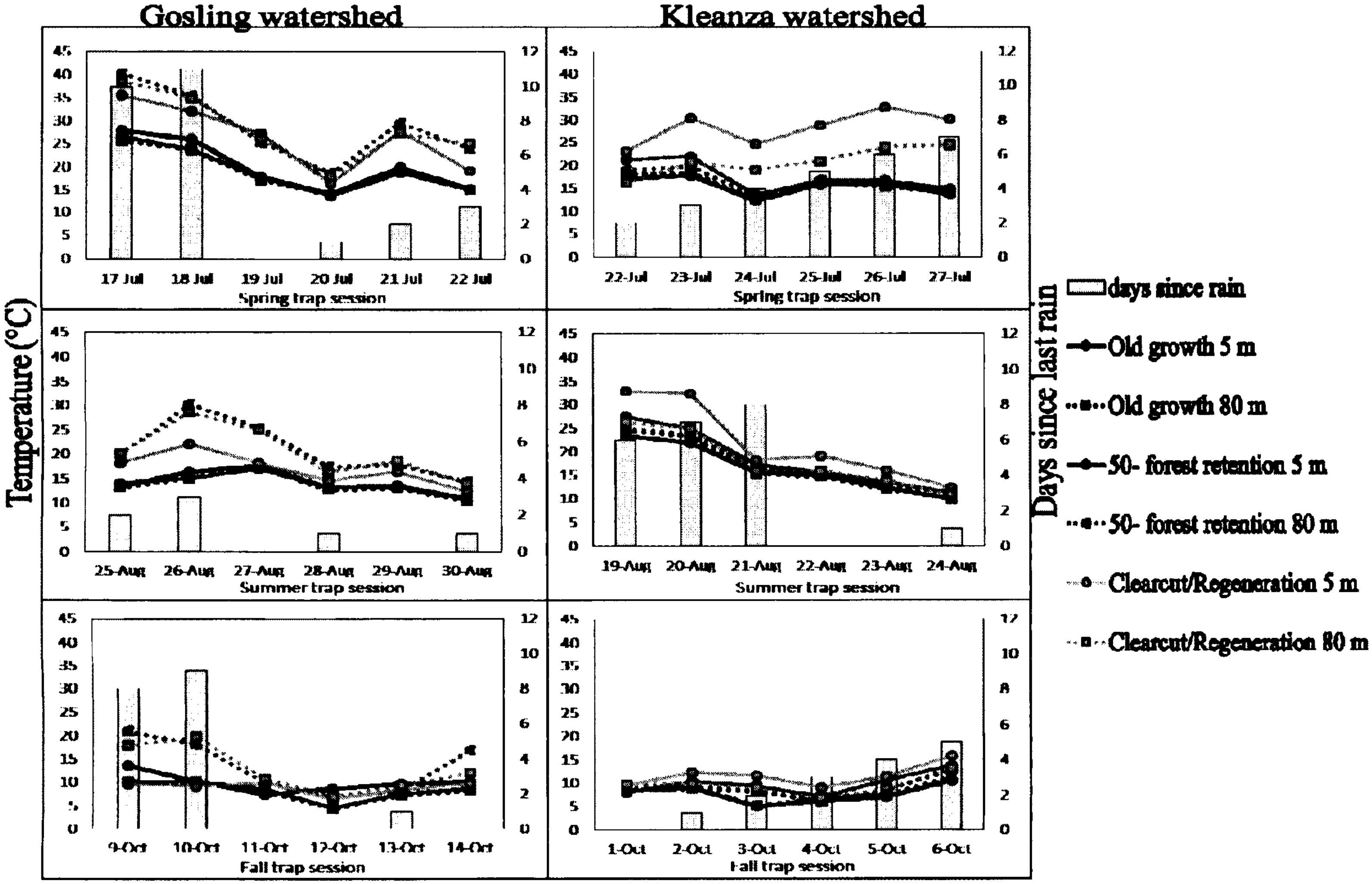
de_transition temp_difference	5	-502.708	1005.415	1015.415	1016.994	63.4	< 0.0001
temp_max temp_max2 site_moisture	7	-505.679	1011.359	1025.359	1028.470	74.9	< 0.0001
temp_difference site_moisture	6	-499.182	998.364	1010.364	1012.634	59.1	< 0.0001
temp_difference canopy_code	6	-503.723	1007.447	1019.447	1021.717	68.2	< 0.0001
de_transition canopy_code days_rain	9	-491.180	982.360	1000.360	1005.654	52.1	< 0.0001
days_rain site_elevation site_elevation2	4	-497.050	994.100	1002.100	1003.126	49.6	< 0.0001
distance_stream densiometer days_rain	4	-478.801	957.603	965.603	966.628	13.1	0.0007
orientation canopy_code days_rain	10	-494.004	988.009	1008.009	1014.675	61.1	< 0.0001
temp_difference site_elevation site_elevation2	4	-494.004	988.008	996.008	997.033	43.5	< 0.0001
orientation days_rain	6	-501.388	1002.775	1014.775	1017.046	63.5	< 0.0001
TREATMENT & TEMPORAL							
orientation trap_month distance_stream	9	-485.514	971.029	989.029	994.323	40.8	< 0.0001
orientation trap_month	8	-510.939	1021.878	1037.878	1041.992	88.4	< 0.0001
orientation trap_month de_transition	11	-502.656	1005.312	1027.312	1035.562	82.0	< 0.0001
trap_month distance_stream	5	-489.550	979.100	989.100	990.679	37.1	< 0.0001
trap_month de_transition	7	-506.661	1013.322	1027.322	1030.433	76.9	< 0.0001
trap_month distance_stream de_transition	8	-487.191	974.383	990.383	994.497	41.0	< 0.0001
site_elevation site_elevation2 trap_month	6	-504.654	1009.307	1021.307	1023.577	70.0	< 0.0001
trap_month densiometer	5	-508.614	1017.229	1027.229	1028.808	75.3	< 0.0001
TREATMENT, ENVIRONMENTAL & TEMPORAL							
trap_month orientation days_rain	9	-496.935	993.870	1011.870	1017.164	63.6	< 0.0001
distance_stream trap_month days_rain	6	-475.193	950.386	962.386	964.656	11.1	0.0020
distance_stream trap_month site_elevation site_elevation2 days_rain	8	-466.747	933.493	949.493	953.608	0.1	0.4908
de_transition trap_month site_elevation site_elevation2 temp_difference	10	-480.949	961.898	981.898	988.565	35.0	< 0.0001
de_transition trap_month days_rain	8	-492.185	984.370	1000.370	1004.484	50.9	< 0.0001
distance_stream densiometer trap_month site_elevation site_elevation2 days_rain	9	-465.125	930.251	948.251	953.545	0.0	0.5064

Appendix II- Logistic regression models used for the 2013 trap data conducted in 2 watersheds located east of Terrace, BC, identifying the distribution of tailed frogs within forest retention treatments.

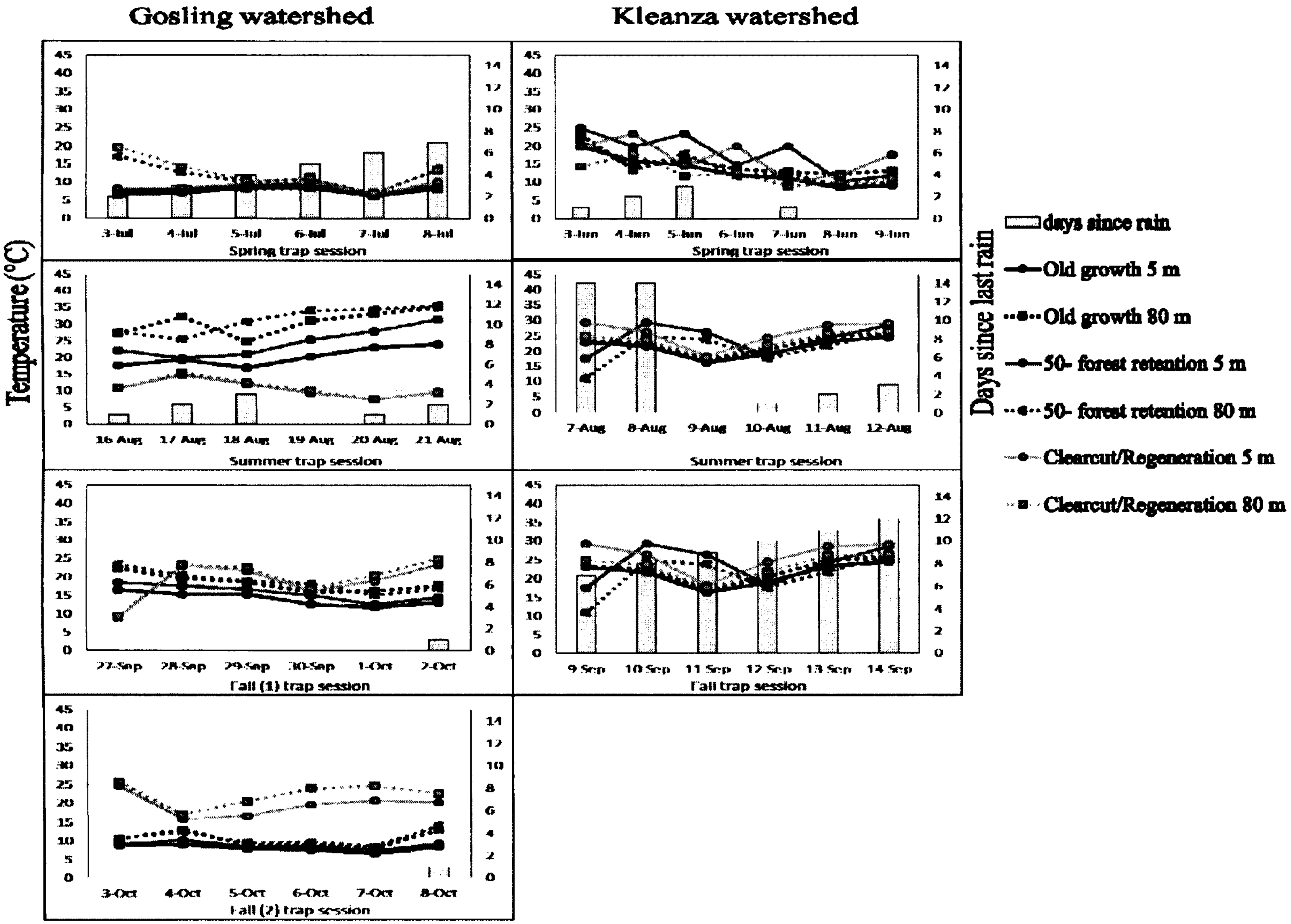
	k	Log Likelihood	-2LL	AIC	AIC$_c$	Δ AIC	AIC weight
TEMPORAL							
code_trap_month (trap_month)	6	-196.277	392.553	404.553	406.8233	40.7	< 0.0001
TREATMENT							
densiometer site_moisture	5	-197.382	394.765	404.765	406.344	40.2	< 0.0001
canopy_code de_transition distance_stream	9	-193.506	387.012	405.012	410.306	44.2	< 0.0001
distance_stream de_transition	5	-195.630	391.260	401.260	402.839	36.7	< 0.0001
site_moisture distance_stream de_transition	9	-194.296	388.591	406.591	411.885	45.7	< 0.0001
distance_stream	2	-198.672	397.343	401.343	401.636	35.5	< 0.0001
site_moisture	5	-198.023	396.046	406.046	407.625	41.5	< 0.0001
de_transition	4	-196.705	393.410	401.410	402.436	36.3	< 0.0001
canopy_code	5	-197.488	394.977	404.977	406.556	40.4	< 0.0001
site_elevation site_elevation2	2	-195.016	390.032	394.032	394.325	28.2	< 0.0001
site_elevation site_elevation2 distance_stream	3	-193.935	387.871	393.871	394.471	28.3	< 0.0001
densiometer	2	-199.021	398.042	402.042	402.335	36.2	< 0.0001
orientation distance_stream de_transition	9	-189.791	379.581	397.581	402.875	36.7	< 0.0001
ENVIRONMENTAL							
temp_difference hum_difference	3	-195.498	390.995	396.995	397.595	31.4	< 0.0001
temp_difference	2	-196.543	393.086	397.086	397.378	31.2	< 0.0001
temp_min temp_min2	3	-198.023	396.045	402.045	402.645	36.5	< 0.0001
temp_max temp_max2	3	-198.746	397.491	403.491	404.091	37.9	< 0.0001
days_rain	2	-185.171	370.343	374.343	374.635	8.5	0.0133
hum_difference	2	-198.477	396.955	400.955	401.248	35.1	< 0.0001
ENVIRONMENTAL & TREATMENT COMBINED							
distance_stream temp_difference	3	-195.838	391.676	397.676	398.276	32.1	< 0.0001
distance_stream hum_difference	3	-197.619	395.238	401.238	401.838	35.7	< 0.0001
de_transition temp_max2 temp_max	6	-195.497	390.994	402.994	405.264	39.1	< 0.0001

de_transition temp_difference	5	-192.911	385.822	395.822	397.401	31.2	< 0.0001
temp_max temp_max2 site_moisture	7	-197.008	394.015	408.015	411.126	45.0	< 0.0001
temp_difference site_moisture	6	-194.730	389.459	401.459	403.729	37.6	< 0.0001
temp_difference canopy_code	6	-192.943	385.886	397.886	400.156	34.0	< 0.0001
de_transition canopy_code days_rain	9	-178.084	356.168	374.168	379.462	13.3	0.0012
days_rain site_elevation site_elevation2	4	-178.563	357.126	365.126	366.152	0.0	0.9262
distance_stream densiometer days_rain	4	-182.718	365.437	373.437	374.462	8.3	0.0145
orientation canopy_code days_rain	10	-177.083	354.167	374.167	380.834	14.7	0.0006
temp_difference site_elevation site_elevation2	3	-190.63614	381.272	387.272	387.872	21.7	< 0.0001
orientation days_rain	6	-180.009	360.019	372.019	374.289	8.1	0.0158
TREATMENT & TEMPORAL							
orientation trap_month distance_stream	11	-189.212	378.424	400.424	408.674	42.5	< 0.0001
orientation trap_month	10	-190.436	380.872	400.872	407.539	41.4	< 0.0001
orientation trap_month de_transition	13	-187.612	375.224	401.224	413.357	47.2	< 0.0001
trap_month distance_stream	7	-195.057	390.113	404.113	407.224	41.1	< 0.0001
trap_month de_transition	9	-193.456	386.912	404.912	410.206	44.1	< 0.0001
trap_month distance_stream de_transition	10	-192.370	384.741	404.741	411.408	45.3	< 0.0001
site_elevation site_elevation2 trap_month	8	-191.637	383.273	399.273	403.388	37.2	< 0.0001
trap_month densiometer	7	-195.260	390.520	404.520	407.631	41.5	< 0.0001
TREATMENT, ENVIRONMENTAL & TEMPORAL							
trap_month orientation days_rain	11	-176.629	353.259	375.259	383.509	17.4	0.0002
distance_stream trap_month days_rain	8	-180.406	360.812	376.812	380.926	14.8	0.0006
distance_stream trap_month site_elevation site_elevation2 days_rain	10	-173.438	346.875	366.875	373.542	7.4	0.0230
de_transition trap_month site_elevation site_elevation2 temp_difference	12	-184.880	369.760	393.760	403.825	37.7	< 0.0001
de_transition trap_month days_rain	10	-178.652	357.305	377.305	383.972	17.8	0.0001
distance_stream densiometer code_trap_month site_elevation site_elevation2 days_rain	11	-173.288	346.577	368.577	376.827	10.7	0.0045

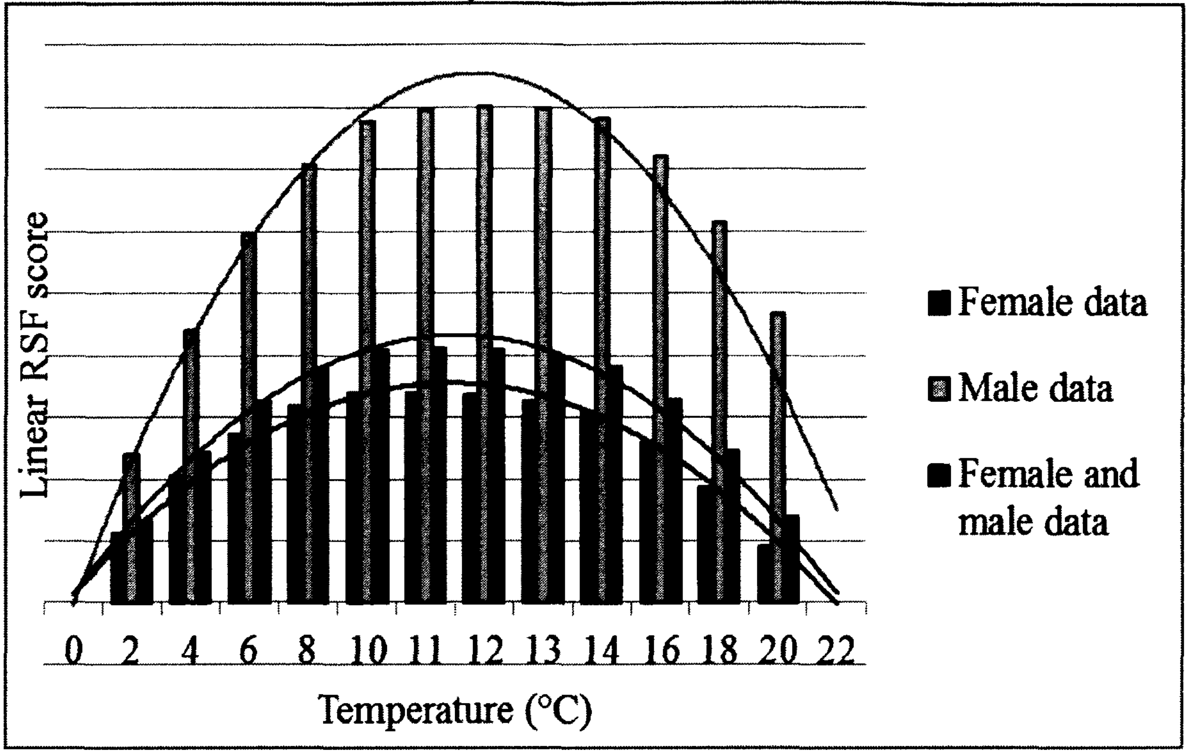
Appendix IV: Temperature and days since last rain at the 5- and 80-m arrays for 4 forest retention treatments in 2 watersheds located east of Terrace, BC during 2012.



Appendix V: Temperature and days since last rain for 5-m and 80-m arrays in 4 forest retention treatments in 2 watersheds located east of Terrace, BC during 2013.



Appendix VI: Graphical representation of optimal temperature of used locations by the tailed frog in 3 watersheds located east of Terrace, BC, during 2011 and 2012. Largest bar represents the optimal temperature for the model based on the Gaussian term (linear and quadratic). The pooled tailed frog model and the female tailed frog model are associated with 11°C, while the male tailed frog data is associated with 12°C.



Appendix VII: Proportion of used locations associated with light levels >103 and <103 lux for each gender across 3 forest retention treatments (old growth, forest retention buffer and clearcut) for 24 radio telemetered frogs in 3 watersheds east of Terrace, BC during 2011 and 2012.

	Female				**Male**			
	Old growth (132)	**Forest retention buffer (91)**	**Clearcut (27)**	**Total (184)**	**Old growth (60)**	**Forest retention buffer (42)**	**Clearcut (0)**	**Total (102)**
< 10^3 lux	93.18	93.41	93.59	90.76	88.33	83.33	0	86.27
> 10^3 lux	6.81	6.59	7.41	9.24	11.67	16.67	0	13.73