

THE EFFECTS OF CLEAR-CUT TIMBER HARVEST ON THE MOVEMENT
PATTERNS OF TAILED FROGS (*ASCAPHUS TRUEI*) IN SOUTHWESTERN
BRITISH COLUMBIA

by

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B.Sc., University of Guelph, 1988

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES

(Faculty of Forestry)

We accept this thesis as conforming
to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA
January 2001

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Date Feb. 28, 2001

Abstract

Pitfall trap grids with drift fences were established in three mature forest stands (>81 years), and three clear-cut sites (<5 years) in the Chilliwack Valley of southwestern British Columbia during June to November 1998 and May 1999, to assess differences in tailed frog (*Ascaphus truei*) abundance and movement patterns. Frog abundance was similar in both habitat types, although immatures comprised 80% of captures in clear-cuts (CC) with bufferless streams, and 51% in mature stands (M). While significantly more adults and subadults were caught in M than CC, the number of immatures captured did not significantly differ between habitat types. However, captures of immatures and subadults did vary significantly between sites within habitat types. Direction of movement by frogs did not differ between habitat types. Capture distances from streamsides also did not differ significantly between habitats, although there were differences between sites within habitat type for immatures. There were more recaptures in M than CC (15% and 2%, respectively). Recaptures in CC were predominantly frogs that returned to traps immediately upon release; in M sites, more recaptures originated from other locations. There were no significant differences in weight (WT) or snout-to-vent length (SVL) between habitat types, although immature WT and SVL differed significantly between sites within habitat types. Similarly, tadpole WT, SVL and snout-to-tail length did not differ significantly between habitat types, while significant differences existed between sites for these measures. The presence of frogs at sites could be predicted from the occurrence of selected plant species and other habitat attributes. Pooled adult numbers were negatively correlated with clear-cut habitat variables (e.g.,

thimbleberry, willowherb thistle), and positively correlated with attributes of mature stands (e.g., leaf litter). Numbers of immatures were negatively correlated with attributes of mature stands (e.g., vine maple), and positively correlated with clear-cut habitat variables (e.g., foamflower). These findings suggest that there are age-specific impacts on tailed frogs in bufferless streams in clear-cuts relative to streams in mature forests. Additionally, variation among sites has a greater influence on immatures than habitat type, which may have long-term implications on population maintenance if survivorship to adulthood also significantly varies between sites. Thus blanket management procedures for tailed frogs (e.g., stream buffers proposed for larval habitat enhancement) will not necessarily be effective for all age classes or for all areas with the same macrohabitat (e.g., clear-cuts).

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Acknowledgements

There are numerous individuals and organisations to which I am gratefully indebted for their assistance with various aspects of this project. Without their contributions, I would never have accomplished this task. Whether it was moral support to keep my spirits up, or sharing their ideas, expertise, equipment, time or knowledge of areas which I had little or no familiarity, every contribution helped to chip away at the block to form something much more tangible.

To these, I graciously thank the following (and my most sincere apologies to anyone that may have been missed): my committee members, Drs. John Richardson, Val LeMay and Charley Krebs; Jamie Smith (External Examiner) and Michael Pitt (Defense Chair). Special thanks to Val for her extreme patience and tolerance in helping me overcome my lack of confidence (pun intended) in statistical methods.

To the dedicated, hard-working field assistants who made the work so much more bearable, I thank Michael Bissonnette, Mark Tressel, Liz Kovics, Robyn Scott, Melanie Grant, Amy Blaylock, and Deb Andrushko.

At UBC, I gratefully acknowledge Drs. Andy Black, Sue Glenn, Elaine Humphrey, Karel Klinka, Bill Neill, Hong Qian, Jordan Rosenfeld, my friends and colleagues in the Centre for Applied Conservation Biology and the Faculty of Forestry, and extra thanks to Anne Casselman, Janelle Curtis, Leo Frid, Liz Gillis, Charlotte Gjerløv, Nancy Mahony, Karl Mallory, Katherine Maxcy, Dan O'Donaghue, Yvonne Patterson, Jeff Shatford, Beth Shields, Christie (Kovacs) Staudhammer, Dave White, Kyle Young and my colleagues in the Richardson lab. Marc Porter, Elke Wind and Katherine Maxcy provided greatly appreciated manuscript comments.

Invaluable support was provided to me by several other individuals and organisations along the way: Guy Fried and Lucy Stad (BC Ministry of Forests), Jan Jonker (Tamihi Logging), Phil O'Conner and Neil Hughes (Coast Mountain Hardwoods), Dean Raven (Scott Paper), Dr. Len Thomas (University of St. Andrews, Scotland), Ken Morton/Vivian Magnuson (DFO Cultus Lake Research Lab), Danny Catt (BCIT), Tracy Reynolds (Vancouver Aquarium), Thomas Lockhart (Westcoast Tattoo), Mr. Herb Dodd and the Dodd Foundation, Heather Adams, Serge Couture, Shane Ford, Eugene Hulak,

Larry and Michi Lee, Marc Porter, Christy (Peterson) Morrissey, Marion Syme, and Michael Tilitzky.

The volunteer field assistants formed the backbone of this project, and while it cost me a fortune in beer, I am indebted to their perseverance and enthusiasm. I wish them all the very best in their career aspirations. Whether it was for a few hours or a few weeks, every little bit cumulatively contributed to overcoming a seemingly monumental task. To this end, I extend my heartfelt thanks to: Monica Belko, Ryan Bell, Joanne Booth, Tara Burke, Brenda Clapham, Chad Davey, Darren Ferguson, David Files, Bruce Fitz-Earle, Joanne Gilchrist, Andy Goel, Tricia Gribbling, Shar Hamm, Corinna Hoodicoff, Leah Jackson, Tom Kagi, Agi Kim, Marjo Laurinolli, Tara LeChasseur, Margo Longland, Jen Lusk, Junjiro Negishi, Mischa Neumann, Caresse Ollenberger, Jeff Omstead, Gary Oppitz, Kelly Pearce, Pam Perreault, Marc and Zach Porter, Larissa Puls, Hilary Quinn, Simone Runyan, Deneen Sawchuk, Tobin Seagel, Beth Shields, Andrea Sirois, Carmen Solis de Ovando, Joe Soluri, Rod Stott, Shannon Stotyn, Andy Swinger, Steve Tordiffe, Carmen Wong, and Jen Young.

Special mention to Tara Burke and Andrea Sirois for their support, compassion and tolerance of my countless lapses of sanity.

I especially would like to thank my family: my father and mother, Bruce and Ruth, and to my sister Debi, who have devotedly supported me through all the endeavours I have ever undertaken, however insane and illogical.

This project was funded through a Forestry Renewal British Columbia grant to Dr. John S. Richardson, to which I am gratefully indebted for not being axed.

Chapter 1. General Introduction

The effective management of any species requires a sound understanding of its habitat use and associations and its role in ecosystem functioning. When ecosystem function is potentially altered by resource extraction (e.g., timber harvest), the full extent of any impacts is often difficult to delineate. To assess the potential impacts on ecosystem components, it is essential that we have an understanding of the linkages between the surrounding environment and the biota that depends on it.

Over the years, there have been escalating concerns over timber harvesting practices in British Columbia (BC), specifically with regards to sustainability and environmental impact. British Columbia has a land base of 95 million hectares, with 59 million hectares covered by forests, a quarter of which has accessible and marketable timber, and of which less than 1% is annually harvested (Ministry of Forests 1996). For the 1997-98 fiscal year, this amounted to a total harvest (public and private) of 173 801 ha (Ministry of Forests 1998). The potential impact of logging on wildlife habitat is therefore enormous. In 1995, the Forest Practices Code of BC (FPC) was introduced to address concerns over the sustainability of provincial forest resources, and any impacts of timber harvest on wildlife habitat. While criticised, the FPC at least recognised previously unconsidered aspects of forest ecosystems that might be impacted by timber harvesting.

Although preservation of biological diversity was a priority in drafting the FPC, presumed habitat requirements for some species could not be ensured within the idealised broad scale coverage that the FPC may have originally sought to achieve. Consequently,

the Identified Wildlife Strategy was developed to address concerns over species and/or habitats overlooked by the initial FPC recommendations (Ministry of Forests 1999). The tailed frog (*Ascaphus truei*) was the only amphibian represented in this strategy. While it recognised that a relationship between forests and *Ascaphus truei* (ASTR) existed, it also became clear that more information was required to assess the full extent of this relationship.

While several studies have assessed logging effects on birds and mammals in BC (e.g., Wetmore *et al.* 1985; Archibald *et al.* 1987; McLellan and Shackleton 1988; Nyberg *et al.* 1989; Kremsater and Bunnell 1992; Schwab and Sinclair 1994; Kinley and Newhouse 1997; Easton and Martin 1998), comparatively little research has been conducted on less visible and (currently) economically unimportant species (e.g., amphibians). Apart from feeding on a variety of arthropods, their sheer biomass alone provides a vast food source available to predatory arthropods, birds, mammals, reptiles, and other amphibians. Their consumption of small invertebrates allows the conversion of otherwise unobtainable energy to be available to larger predators when they in turn are ingested (Pough 1980; Pough *et al.* 1987). Thus any environmental effect that limits amphibian population growth or persistence may ultimately lead to further impacts throughout the ecosystem.

With growing evidence of worldwide amphibian declines (Wake 1991; Blaustein *et al.* 1994; Pechmann *et al.* 1994; Blaustein and Wake 1995; Houlahan *et al.* 2000), it is important to assess whether potential sources of local decline are contributing to an international conservation dilemma. Although timber harvesting may not be the single greatest contributor to overall amphibian declines (Bunnell *et al.* 1997), it is important to

determine what effects, if any, such impacts may be having within our own borders. Previous studies evaluating logging impacts on amphibians have found measures of density, abundance, biomass and/or species richness to be negatively correlated with factors such as increased air and water temperatures, exposure to sunlight, predators, vulnerability to windfalls, bank erosion and reduced water flow rates in streams (e.g., Blaustein *et al.* 1995; deMaynadier and Hunter 1995; Dupuis *et al.* 1995; Bull and Carter 1996; Wahbe 1996; Johnston 1998; Richardson and Neill 1998; Dupuis and Steventon 1999; Lemckert 1999). However, due to the variation in responses observed, sometimes within the same species, the full extent of logging impacts on amphibians is difficult to determine (see deMaynadier and Hunter (1995) for a review). Regional variation seems to add to the confusion. In BC for example, the physical and biological uniqueness provided by a diversity of habitats (Ministry of Forests 1994), may result in different population responses than that observed elsewhere in Canada or the Pacific Northwest.

In Canada, the tailed frog is found only in BC, generally associated with streams within limited areas of the Coastal Western Hemlock and Engelmann Spruce/Subalpine Fir biogeoclimatic zones (Dupuis *et al.* 2000). Thus, understanding its relationship with our coastal forests is essential to manage the species and its habitat while implementing forest management practices in an economical, environmentally sound, and sustainable manner. For the most part, effective, scientifically scrutinised management regulations are still lacking for the tailed frog. This results largely from the paucity of information about the extent of the relationship between ASTR and forests in BC, particularly life stages and movement activity post-metamorphosis. ASTR are patchily distributed throughout the Pacific Northwest (Blaustein *et al.* 1995), a situation possibly enhanced by

philopatry (Daugherty and Sheldon 1982b). Habitat fragmentation from logging may further isolate these “patches” of frogs (i.e., pockets of high densities surrounded by areas with no frogs). Identifying causal mechanisms underlying movement activity may reduce such isolation as well as reveal shifts in population dynamics (Merrell 1970; Daugherty and Sheldon 1982b; Slatkin 1985) as animals evolve or respond to changing environmental conditions in order to survive (Endler 1977; Jackson *et al.* 1999).

Movement patterns and rates occur on a variety of scales, and may shift with changing environmental conditions. The range of movement in animals can greatly vary, from those demonstrating strong philopatry to their natal area, to those that demonstrate little to no site fidelity, (e.g., nomadism; Wiens 1976; Sinclair 1983). Natal dispersal is the movement an animal makes from its birthplace to where it reproduces (Caughley and Sinclair 1994). Usually it is a one-way movement in which individuals leave their site of origin, never to return (Zug 1993). In most situations, movement allows animals to relocate to more favourable conditions, thus increasing survival and fitness (Schwarzkopf and Alford 1999). Thus, movements may be cyclic or seasonal, for reasons such as foraging or hibernation (Duellman and Trueb 1994). If animals survive, then two-way migration occurs if individuals return to their area of origin (Zug 1993). It is not known to what extent, if any, two-way migration occurs in ASTR. While some species may migrate between winter and summer ranges, others only demonstrate local movement within a relatively localised, home range (Caughley and Sinclair 1994). This study will focus on the latter, on movements after metamorphosis, a life stage that has been relatively overlooked in previous studies, especially in BC.

The main focus of this thesis will assess movement patterns of juvenile and adult ASTR in clear-cuts¹ (CC) and mature (M) forest stands, and determine whether any differences in movement exist between habitat types and/or frog age classes. Habitat relationships will also be examined to determine which habitat attributes contribute to movement patterns. While habitats are likely to vary considerably between forest treatments, identifying the most important features that influence habitat use may provide insight as to the most practical management strategies for a species. A summary section will link results from both sections, and provide recommendations that managers can implement to manage ASTR populations during timber harvesting.

While this study focuses on tailed frogs, the species only represents a test case for comparing differences in movement patterns between and within two habitat types. The issues being addressed, and the general approach to the analysis can be applied to any other group of animals (with species-specific adjustments). Findings from such studies can provide essential information to managers that can be practically applied to effectively and sustainably, manage our natural resources.

¹ The BC Ministry of Forests (1995b) defines a “clearcut” as “a silvicultural system that removes an entire stand of trees from an area of one hectare or more and greater than two mature tree heights in width, in a single harvesting operation.”

Chapter 2. Movement patterns of metamorphosed tailed frogs in clear-cuts and mature forest stands

Introduction

Movement activity is fundamental to the survival and evolution of a species (Endler 1977; Daugherty and Sheldon 1982b), and may reflect responses to changing environmental conditions (Jackson *et al.* 1999). Assessing individual movement patterns provides insight on population dynamics and issues dealing with habitat management, gene flow, metapopulation dynamics and population maintenance (Merrell 1970; Daugherty and Sheldon 1982b; Slatkin 1985). This information can then be used to devise effective management plans for a species and the habitats with which they are associated. Understanding rates and direction of movement, and potential causal mechanisms, also allows managers to evaluate the potential resilience of populations to disturbances (Townsend and Hildrew 1994), whether natural or human induced.

For amphibians, physiological constraints play a major role in influencing movement. Their dependence on moisture and exploitation of different habitats during their life cycle has led to their consideration as indicators of environmental health (Wake 1991; Blaustein *et al.* 1995; deMaynadier and Hunter 1995; Welsh and Ollivier 1998). However, their small size and subsequent lower visibility make them more difficult to track than larger vertebrates. Nonetheless, knowing their movements in habitats pre- and post-disturbance helps to assess the effectiveness of conservation and management applications, particularly in situations where disturbance is human-induced (e.g., during timber harvesting).

Of particular concern is whether habitat use varies between different habitat types (e.g., riparian and upland areas) when alteration such as logging occurs. Without knowledge of movements within and between habitats, preservation of one habitat type (e.g., riparian habitats only) may not provide sufficient protection for a species if adjacent habitat (e.g., upland) is equally required during the life cycle but left unprotected. The effects that disturbances such as timber harvest may have on habitat use or movement through an area is thus vital to our understanding of population dynamics within these landscapes (deMaynadier and Hunter 1999).

The impacts that a disturbance has on an ecosystem and its associated species will vary temporally and spatially. Definitions of disturbance vary in ecological studies (see Townsend and Hildrew (1994) for an overview). For this study, disturbance is defined as the disruption of an ecosystem, community or population structure and changes in available resources, substrate availability or the physical environment (White and Pickett 1985; Krebs 1994). Although timber harvesting is itself a disturbance, it also causes further environmental perturbations (e.g., susceptibility to increased erosion/slope failure, windfall, etc.). These perturbations can vary in magnitude and frequency, and their effects on any given species will depend partly on its scale relative to the size (i.e., abundance, density) and generation time of the organism(s) concerned (Townsend and Hildrew 1994).

Within the Pacific Northwest, logging practices generally reduce larval and adult tailed frog (*Ascaphus truei*) populations (Bury and Corn 1988; Corn and Bury 1989; Aubry and Hall 1991; Bury *et al.* 1991b; Corn and Bury 1991; Blaustein *et al.* 1995; Bull and Carter 1996; Wahbe 1996; Dupuis and Steventon 1999). However, it could not be

determined whether logging activity directly influenced the declines due to habitat degradation, or whether declines in these areas were a result of disrupted immigration. It is likely that a combination of factors may be acting on population responses. In the absence of long-term data, the full extent of such impacts and any population responses will not be known.

deMaynadier and Hunter (1995) analysed the results of 18 studies examining the effects of clear-cutting on amphibians and found a 3.5-fold median difference in abundance between controls and clear-cuts. However, long-term effects of forest harvesting on amphibians vary with forest age, and the quantity of intact microhabitat available (deMaynadier and Hunter 1995). Welsh (1990) found five species of amphibians to have significantly higher abundances on older sites, while three species (tailed frog, Del Norte salamander and Torrent salamander) were uncommon or absent in younger sites. While some studies have supported the findings of higher abundances of salamanders in older forests (e.g., Raphael 1988; Welsh and Lind 1988, 1991; Corn and Bury 1991; Dupuis *et al.* 1995), others have found there to be no difference in abundance of salamanders (Aubry *et al.* 1988) or anurans (e.g., Raphael 1988). Thus general interpretations are difficult to qualify, and may be further confounded when broken down by gender, age class or seasonal oscillations.

For example, larval amphibian densities may be greater in clear-cut streams than old growth streams (Hawkins *et al.* 1983; Richardson and Neill 1998), an observation recorded in fish (Murphy and Hall 1981; Bisson and Sedell 1984). In order to effectively manage a species closely associated with forest stands, it is important to know its life history strategies at all ages, including differences in movement activities, abundance,

habitat use, and which factors influence shifts in habitat use. Amphibians are known to follow distinct “corridors” (Stenhouse 1985; Verrell 1987; Rosenberg *et al.* 1998), particularly between their aquatic and terrestrial habitats (Martof 1953; Shoop 1968; Phillips and Sexton 1989; Rudolph and Dickson 1990) and such activities will vary seasonally (e.g., Hurlbert 1970; Healy 1975; Gill 1978b). Migration rates also differ by size (e.g., Martof 1953; Hurlbert 1970) and sex (e.g., Healy 1975; Phillips and Sexton 1989; Sexton *et al.* 1990; Dodd and Cade 1998). However, Daugherty and Sheldon (1982b) found no evidence of seasonal or directional movement in *Ascaphus truei*, nor significant differences between sexes, although pre-reproductive individuals moved greater distances than adults. Thus, movements may be stage dependent in ASTR, although no studies have verified this. Landreth and Ferguson (1967) revealed that metamorphosed ASTR are able to use celestial and visual cues for orientation, which are likely used upon emergence to seek favourable habitat, as has been observed in toads and newts (Dodd and Cade 1998). Knowledge of stage-dependent movement may have great bearing on population demography as differences in movement rates and direction between various ages and sex classes may indicate which life stages are critical to population maintenance (Mduma *et al.* 1999).

Researchers who have studied ASTR larval stages have proposed hypotheses as to the mechanisms behind tailed frog movements post-metamorphosis, although few of these have ever been field-tested. *Ascaphus* may move upstream to headwater creeks for summer refuge (Metter 1964) or for females to lay eggs (Brown 1975). Others found that frogs moved downstream to larger creeks, possibly to facilitate breeding in more stable waterways rather than small headwaters prone to drying up (Landreth and Ferguson

1967). However, none of these studies focused on movement differences between different life stages.

Distribution, Ecology and Life History of *Ascaphus truei*

The tailed frog is endemic to Pacific northwestern North America. In BC, it is found within the Coastal Western Hemlock, Interior Coastal Hemlock and Mountain Hemlock biogeoclimatic zones (Meidinger and Pojar 1991). There is also an isolated set of populations in the south Kootenays of BC falling within the Engelman Spruce-Subalpine Fir zone (Ministry of Forests 1997). Within British Columbia, the species is provincially blue-listed (vulnerable) by the BC Conservation Data Centre (Cannings *et al.* 1999). If salmonid habitat exists downstream, some level of protection may be provided by the federal Fisheries Act (Dupuis and Bunnell 1997). Otherwise, tailed frogs are protected provincially under the same blanket regulations for all native terrestrial vertebrates by the BC Wildlife Act. The FPC also addresses the preservation of their habitat through the designation of Wildlife Habitat Areas in the Identified Wildlife Strategy (Ministry of Forests 1999).

Tailed frogs have the longest lifespan (15-20 years), larval period (1-4 years), and age to sexual maturity (7-8 years) of all North American frogs (Daugherty and Sheldon 1982a; Nussbaum *et al.* 1983; Bury and Adams 1999). All life stages have narrow temperature tolerances, with adults reaching lethal temperatures at about 20-22°C (Metter 1966; Landreth and Ferguson 1967; deVlaming and Bury 1970). It is the only North American frog that requires cold, clear, fast-flowing mountain streams to develop, and is more prone to desiccation than most other anurans (Daugherty and Sheldon 1982a; Nussbaum *et al.* 1983). Their susceptibility to desiccation results from a strong

dependence on vascularized skin for respiration (Claussen 1973a; Claussen 1973b). Respiration through the skin works well in fast-flowing, oxygen-rich, aquatic systems. As survival and movement are dependent upon the availability of a cool, moist, terrestrial environment (Hawkins *et al.* 1988), metamorphs are elusive. They are well-camouflaged, live in remote mountain streams, and predominantly forage at night along the creek and in the damp, surrounding riparian zone (Nussbaum *et al.* 1983; Capula 1989; Leonard *et al.* 1993).

Objectives and Predictions

The main purpose of this study was to assess whether clear-cut timber harvest influences the movement of metamorphosed tailed frogs compared to movement in relatively less disturbed, mature forest stands.

The hypotheses and predictions are based on the assumption that tailed frogs depend upon riparian habitat for at least some part of their life cycle to develop, and that any alteration of this habitat may impact on populations using the area.

If clear-cutting decreases habitat availability for species associated with riparian habitats, then species such as ASTR will use narrower strips of the riparian zone, and may become restricted to upstream and downstream movements within the riparian corridor in clear-cut streams. It is further predicted that the main dispersers moving within both mature forests and clear-cut sites will be pre-reproductive immatures, while more adults are expected to remain philopatric along streamsides in both habitats (Daugherty and Sheldon 1982b). Thus, strong directionality in frog movement is not expected to occur in mature forest stands with intact overhead canopy.

In summary, the specific hypotheses being addressed as a consequence of habitat alteration include:

1. Movements in clear-cut (altered) areas have a greater upstream/downstream component within riparian zones compared to less disturbed, mature forests,
2. Tailed frog abundance is lower in clear-cuts than in intact forest, and,
3. Pre-reproductive immature frogs are the main dispersers.

Study Area

Three replicates each of clear-cut habitats (< 5 years old at time of study) and mature second growth sites (>81 years) were established in the Chilliwack Valley of southwestern British Columbia. This area lies within the Coastal Western Hemlock biogeoclimatic zone of British Columbia (Meidinger and Pojar 1991), within the Cascade Range approximately 120 km east of Vancouver. These sites were selected based on access and feasibility of installing pitfall trap stations (Corn and Bury 1990), alongside S6 streams (<3 m wide, non-fish bearing)(Ministry of Forests 1995a), where preliminary surveys revealed the presence of tailed frog larvae. Trap grids in clear-cut sites (CC) were located beside creeks without buffer strips, with sites referred to as Tamihi, McTam and McGuire. Trap grids in the mature forest stands (M) were referred to as Ford, Elk and Vedder (Table 2.1 [pg.38]; see Appendix 1 [pg.99] for site details).

Methods

Sixteen pitfall stations were established in each study site, spaced 20-m apart in a 4x4 grid pattern (Figure 2.1a) [pg.44] incorporating systematic sampling. Each station

consisted of clusters of four pitfall traps quartered by four guiding "drift" fences arranged in an "X" pattern such that direction of movement could be determined (upstream, downstream, towards or away from the stream). Stations closest to the streams were within 5-m of the streamside. If a station could not be established due to barriers such as stumps or trees, the location was shifted slightly around the barrier, but still within 3-m of its originally designated location. Obstacles blocking drift fences such as logs or rocks were removed or cut wide enough to allow passage of the drift fence and a corridor on either side. Where necessary, drift fences were diverted slightly around large, non-movable obstacles (e.g., stumps, trees) and when possible, natural barriers such as fallen logs in their original position were incorporated into use as natural drift fences. Fences were cut from medium weight, clear polyfilm plastic sheets 25 cm high, and extended 5 m out from the centre of the trap station (Figure 2.1*b*) [pg.44]. The bottom of each fence was buried for 5 cm, and fences were stapled onto 50 cm wooden stakes pounded into the ground at intervals sufficient to prevent sagging. Pitfall traps were fashioned from 40-cm lengths of polyvinyl chloride (PVC) piping (15.2 cm diameter) buried upright with tops flush with the surface. Bottoms were cut from black PVC sheeting and sealed with non-toxic aquarium caulking (General Electric RTV silicone rubber adhesive sealant) into one end of the PVC pipe. Approximately 5-8 holes (3 mm diameter) were drilled into each bottom to allow drainage but prevent amphibian escapes. Plastic margarine containers (no. 2 size, 907 g capacity; Granpac, Wetaskiwin, Alta.) with bottoms cut out, were wedged into the top inner portion of each trap, with tops flush with the top of each trap, which in turn was flush with the surrounding soil. This provided a "lip" to prevent climbing amphibians from escaping. A length of biodegradable, heavy jute twine

(Bridgeline Ropes, Trenton, Ont.) extended down to the bottom of each trap, fastened to the top by tying a knot in the end and wedging it into a slit cut in the top of the margarine container. This twine allowed small mammals to climb out and reduced predation on amphibians by trapped mammals, yet minimised the chances of amphibian escape. Although traps were deep enough to provide sufficient shade to maintain relatively cool temperatures, pieces of moss were placed in the bottom of each trap and moistened with stream water, to provide cover and reduce vulnerability to desiccation. To minimise exposure to pesticide residues when clear-cut sites were sprayed with glyphosate in September 1998, moss was removed and replaced with moistened sponges (Greenburg *et al.* 1994) from September-November 1998. While there was no evidence of pesticide residue present, this step was taken as a precautionary measure.

A total of 384 pitfall traps and drift fences were used for the six study sites. Each week, traps were left open for three consecutive nights and checked the next morning. Checking traps within 24 hours was chosen to minimise observer effects and decrease the likelihood of amphibians becoming desiccated or eaten by mammals during prolonged periods in the traps. Trapping occurred from June to September 1998, with traps closed between each 3 day/3 night trapping session. A similar 3 day/3 night trapping cycle was also conducted during May 1999. Traps were closed by fastening plastic lids onto the margarine containers, then securing the container down by rocks or logs. Due to driving distances between sites, only three trap grids were left open at a time from June to September. With the onset of increased precipitation and cool weather in October and November 1998, traps were continually left open at all sites and checked approximately once every 4 days.

Mark/Recapture

All captured frogs from pitfalls and larvae from stream surveys were weighed (± 0.05 g) using an Ohaus[®] SC2020 electronic balance. A 20-g Pesola[®] hand-held scale was also used during times of heavy rainfall or wind, or when batteries in the balance failed. Snout-to-vent (SVL) and snout-to-tail (STL) length were measured using Vernier[®] calipers or a clear plastic ruler. Each individual was sexed and aged visually. All metamorphosed frogs were marked by the injection of a coloured, non-toxic elastomer dye (Northwest Marine Technology, Inc., Olympia, WA) under the ventral skin surface of the hind leg, then individually marked by toe-clipping (Ferner 1979; Sutherland 1996). Trapped frogs were released in the quadrant opposite to where they were caught at least 1-m away and facing away from the traps as this was the presumed, intended direction of movement. Individuals caught outside the pitfall traps, were released at their point of capture.

Transect Surveys

Within each site, pitfall sampling was conducted in conjunction with walk-through, visual encounter surveys (VES) along pre-flagged transect lines. In the clear-cut sites, vegetation was cleared from these transect lines with a brushcutter to facilitate visibility and for safety considerations when conducting surveys after dark. VES were time-constrained to a maximum of two hours, and included one transect along the streamside, three transects 10-metres outside and parallel to the outer boundaries of the trap grid, and two surveys through the middle of the grid along the two middle trap lines perpendicular to the stream. Vegetation was not cleared from transect lines alongside the streams. The purpose of the VES was two-fold: (1) to provide a measure of the

effectiveness of the pitfall traps (i.e., if significantly more frogs were encountered during VES than were caught in the traps, this indicated the pitfalls were inadequate to sample ASTR), and (2) to evaluate the numbers of frogs moving out of the main grid, as a limited measure of emigration from the main study area, as opposed to losses due to mortality. This issue has not been addressed in previous studies of ASTR in Canada. VES were conducted after dark, during twilight and dusk, and during daylight hours at each site to determine peaks in activity levels between diurnal and nocturnal periods. Cursory surveys conducted after dark employed the use of both high-powered diving lights to illuminate a large area, or lower intensity, battery-powered Petzl® headlamps to catch amphibian eyeshine. To minimise habitat impacts, surveys were conducted in a cursory manner.

Larval Surveys

For each stream, intensive surveys of larval abundance were conducted every two months to estimate the proportion of frogs metamorphosing in each site. Stream surveys were conducted along 100 m reaches of the stream adjacent to the pitfall grid. The stream was divided into ten 10 m sections, each of which was intensively surveyed by an individual by lifting rocks and logs within the streambed and holding a dipnet downstream to catch loosened larvae. Each larva captured was weighed and its SVL and STL measured. All larvae were then returned to their respective stream sections after the survey. Numbers per metre of stream length were determined for each stream and then compared to the number of metamorphosed frogs caught within the site to determine the ratio of larvae present to the number of metamorphs. This measure provided a control for differences in stream productivity.

Data Analysis

All frogs captured were sexed (male, female or unknown). As ages of transformed *Ascaphus* are difficult to qualify (Daugherty and Sheldon 1982a), age classes were defined as adult (reproductive), immature (pre-reproductive), or subadult (breeding capacity unknown). While previous studies have aged *Ascaphus* by length measurements (Bull and Carter 1996), weights were used in this study as SVL and STL were highly subject to observer bias (e.g., if the frog was compressed when it was being measured). Frogs weighing >4.0 g were considered as adult, subadults were 1.76-3.99 g, and immatures were 1.75 g or less.

For all statistical analyses, significance levels of tests were set at $\alpha = 0.05$. A multivariate analysis of variance (MANOVA) was performed on log-transformed weight (WT) and rank transformed SVL data using the General Linear Models Procedure (SAS 1994), to evaluate differences between habitat types and sites among the different age classes and sexes. As SVL and STL are basically the same measure in all groupings except males with a discernible "tail," STL was not used in the analysis of metamorphosed frogs. The analysis for SVL and WT of metamorphosed frogs used the combined capture data from pitfall traps and those caught during tadpole stream surveys. For tadpole data, a MANOVA was also performed using the General Linear Models Procedure (SAS 1994), after SVL, STL, and WT data were rank-transformed for normality.

For pitfall captures at each site, the numbers of frogs in each age category were recorded for each direction (upstream, downstream, away from creek, towards creek) and distance from streamside (5-m, 25-m, 45-m, 65-m).

If count data for each age class were not normally distributed (based on Wilk's Lambda), then data were $\ln(x + 1)$ or rank transformed to obtain normality using the General Linear Models Procedure (SAS 1994). The Least Square Means was used in the Analysis of Variance (ANOVA) for direction analysis or Analysis of Covariance (ANCOVA) for distance data (with distance from streamside as the covariate)(SAS 1994).

A Goodness of Fit Chi Square analysis (Sokal and Rohlf 1983) was used to assess differences in the number of recaptures between clear-cuts and mature stands. The Fisher Exact test (Daniel 1978) was used to compare the proportion of recaptures coming from elsewhere within the study grid to those that were simply turning around and being recaptured at the same pitfall station from which they were released.

Results

Pitfall traps successfully captured *Ascaphus* and other amphibians. Seven species were caught in clear-cuts and ten in mature stands (see Appendix 2) [pg.100]. Tamihi was the only site at which *Ascaphus truei* was the only amphibian caught in the pitfall traps. Pacific Giant Salamanders (*Dicamptodon tenebrosus*) were detected in all streams except Ford, although terrestrial forms were only captured by pitfall traps in the mature stands. Tailed frog capture rates were highest during the spring and fall months (Figure 2.2) [pg.45]. Rates decreased after June, coinciding with hot, dry weather, then increased in October, coinciding with increasing precipitation (see Chapter 3 for an analysis of environmental variables). A total of 88 frogs were caught in pitfalls in mature stands and 87 in the clear-cut sites during the study period, not including recaptures. Although

overall total captures did not vary between habitat types, with immatures comprised 80% of the total captures in clear-cuts and 51% in mature stands. For immatures, 76% were caught in the Tamihi clear-cut (Table 2.2) [pg.39].

Mark/Recapture

Of the 175 frogs caught in pitfall traps during the study, 16% were recaptured in mature stands and 8% in clear-cuts. If frogs are excluded that returned to the nearest pitfall trap within 24 hours (i.e., those that turned around and fell back into the trap immediately upon release), then recapture rates amount to 15% for M recaptures and 2% for CC recaptures. Significantly more frogs were recaptured in mature stands than in the clear-cuts ($\chi^2 = 8.695$, one-tailed). A significantly greater proportion ($p < 0.05$) of recaptures in the clear-cuts were frogs that simply turned around and fell back into the pitfall traps, whereas recaptures in mature stands were frogs that were previously captured from other pitfall stations within the trap grid (Table 2.3) [pg.39].

Transect Surveys

During the study period, 21 VESs were conducted at the sites, with a minimum of three VESs at each study grid, during daytime, after dark, and twilight hours. These surveys resulted in only one *Ascaphus* capture. Due to safety considerations, fatigue, and the low return-for-effort rate, VES were deemed inefficient for sampling *Ascaphus* at the sites and surveys were discontinued after July 1998.

Direction of movement

For directional data, ANOVA on $\ln(x + 1)$ -transformed data indicated a significant effect of habitat type and site within habitat type on total frog captures (Table 2.4) [pg.39]. Further breakdown by frog age class revealed that more subadults were caught in mature stands than clear-cuts ($p=0.04$). Although more adults were caught in mature stands, the difference was not significant (Table 2.4) [pg.39]. For adults, $\ln(x + 1)$ -transformed data did not meet all the assumptions of normality. However, as the departure from normality was not considered to be extreme ($p=0.03$), the level of significance and the power of the test were still considered as valid (Neter and Wasserman 1974). Habitat type was weakly associated with immatures, although there was a significant effect of site nested within habitat (Table 2.4) [pg.39]. This pattern also occurred with subadults. For immatures, the Bonferroni test indicated that more frogs were caught in Tamihi than all other sites except Elk (Table 2.5) [pg.40]. Within the mature stands, there was no difference in numbers of immatures captured between the sites. Similarly, the Bonferroni test indicated that significantly more subadults were caught in Elk than McTam ($p=0.002$) and McGuire ($p=0.002$). No other site comparisons were significant. From the four movement directions that were compared at each site (upstream, downstream, towards the stream, away from the stream), the ANOVA indicated that there was no effect of habitat type on movement direction for any age class (Table 2.4) [pg.39]. In both habitats, the fewest number of frogs moved away from the stream (13% in M, 11% in CC; Table 2.6) [pg.40]. Overall, more frogs moved parallel to

the stream (55% in M, 68% in CC; Table 2.6) [pg.40] than perpendicular (Figure 2.3) [pg.46], although these differences were not significant.

Distance from streamside

The ANCOVA for total frogs $\ln(x+1)$ -transformed data (with distance as a covariate), also indicated a significant effect of site within the habitat (Table 2.7) [pg.40]. Further breakdown by age class supported the pattern of significantly more adults being caught in mature stands than clear-cuts (Figure 2.4 [pg.47]; Table 2.4 [pg.39]). As $\ln(x+1)$ -transformed data for subadults did not meet the assumptions of normality, likely a result of low captures, data were rank-transformed and made closer to normality ($p=0.02$). No significant differences in distances were observed for subadults. Similar to the direction analysis, immatures were more affected by site than by habitat type, and the Bonferroni test again indicated that the Tamihi site had significantly higher numbers than all other sites except Elk. Distance of capture from streamside was also significantly affected by site nested within habitat type for immatures (Table 2.7) [pg.40].

For the immatures, the ANCOVA revealed that the slopes and intercepts of the regression lines changed by site (Figure 2.5) [pg.48]. Although the number of captures increased slightly with distance from streamside for Tamihi and Ford, McGuire had no relation with distance. At all other sites, capture rate decreased with distance from streamside.

Body size and larval surveys

When \log_{10} WT values for all frog captures was plotted against SVL, it became clear that WT distinguished age classes more clearly than SVL, where a great deal more overlap occurred (Figure 2.6) [pg.49]. The MANOVA indicated that there were no significant differences in mean WT or SVL between habitat types for any of the age classes (Figures 2.7 and 2.8) [pg.50]. However, as with the direction and distance analyses, there was significant variation between sites for WT and SVL of immatures. Immature WT was significantly greater in Ford than Vedder or McTam ($p < 0.0001$). For immature SVL, Vedder was significantly lower than Tamihi or Ford (also $p < 0.0001$; see Table 2.8) [pg.41].

As gender is difficult to assess with ages other than adults, there was a relatively high proportion of unknowns, as adults only comprised 27% of the total captures. Thus sex ratios could only be determined for adults, with an overall higher mean ratio of male:female captures in both habitat types (2:1 in CC, 8:3 in M; Table 2.8) [pg.41]. Regardless of habitat, the site with the greatest number of adults also had the highest ratio of male:female captures when compared to other sites within the same habitat type (for CC, 7:3 in McTam, for M, 14:5 in Elk; Table 2.8) [pg.41]. ANOVA analyses were also performed on the gender data, but after various transformations, a normal distribution was not obtained, likely a result of low capture rates. Thus the analyses were not carried any further with the gender data.

For tadpoles, no significant difference between habitat types was revealed by the MANOVA performed on rank-transformed WT ($p = 0.70$), SVL ($p = 0.82$), and STL ($p = 0.77$), although significant variation did exist between sites ($p = 0.0001$ for all

measures; Table 2.9) [pg.42]. For WT, tadpoles in Tamihi were significantly smaller than all other sites ($n=15$; $p<0.003$), and Elk tadpoles weighed significantly less than those in McTam ($p=0.0003$) and McGuire ($p=0.0006$; Table 2.10) [pg.42]. Similarly, SVL was also significantly lower for Tamihi compared to all other sites, although McGuire tadpoles had a significantly greater SVL when compared to Elk tadpoles (Table 2.11) [pg.42]. Greater variability occurred in STL measures. McTam tadpole length was significantly greater than Tamihi, Elk and Ford, with Tamihi also having a significantly lower STL than Elk and Vedder (Table 2.12) [pg.43].

For clear-cuts, regression analysis revealed a strong association between the numbers of frogs caught by pitfall traps at each site and the numbers of tadpoles caught in the corresponding stream during stream surveys ($r^2 = 0.99$; Figure 2.9 [pg.51], Table 2.13 [pg.43]). For mature stands, the regression indicated that there was a very weak relationship between stream tadpoles and corresponding pitfall frog captures ($r^2 = 0.002$; Figure 2.9 [pg.51], Table 2.13 [pg.43]). This led to a moderate relationship being reflected between tadpole numbers and pitfall frog captures over all six sites ($r^2 = 0.33$; Figure 2.9) [pg.51]. Thus, as a result of the tadpoles being poor predictors of the number of metamorphosed frogs in mature stands, the overall regression indicated that tadpoles were not good predictors of metamorphs across both habitat types combined.

Discussion

These findings indicate that clear-cut streams without buffers affect the distribution of different age classes of *Ascaphus truei*. Adult and subadult abundance was higher in mature stands. Although more immatures were captured in clear-cuts, immatures were more influenced by site than by habitat type. The variation among sites observed for immatures was largely a result of the high abundance of immatures caught in the Tamihi clear-cut. *Ascaphus* may have a greater probability of surviving to adulthood in mature stands than in clear-cuts or, perhaps emigration rates out of clear-cuts are greater but could not be detected in this study. Alternatively, there exists the chance that the Tamihi stream may be a source stream with exceptionally favourable habitat. It is difficult to assess any long-term effects on population structure without knowing how numbers and age classes are regulated within *Ascaphus* populations. This would require knowledge of age-specific mortality rates, and the extent to which density dependence is occurring (Mduma *et al.* 1999).

Mark/Recapture

The relatively low recapture rates found in this study may indicate that frogs moving through the site were new individuals, trap shyness was occurring (Sutherland 1996), there was a high mortality rate, encounter rates were low due to minimal movement, or some combination of these. While low recapture rates did not allow any inferences of population estimates, there were significantly more recaptures in mature stands than clear-cuts. One possibility may be a higher mortality rate in clear-cuts relative to that of mature forest stands. For immatures, this effect may be magnified due

to a greater vulnerability to desiccation owing to a smaller body size (high surface:volume ratio) and their semi-permeable skin (Bellis 1962). Alternatively, behavioural patterns may differ in clear-cuts such that frogs are less likely to be caught (i.e., lower movement rates or trap shyness). If conditions were more conducive to the physiological limitations of tailed frogs in mature stands, then greater activity in these sites would increase the probability of being caught.

The analysis of the Fisher Exact test is more open to interpretation. The significantly greater ratio of frogs turning around and being recaptured at the same trap station in the clear-cut sites suggests that frogs are disoriented in these sites, lack alternative refuges, or perhaps there is some form of habitat philopatry occurring. While Daugherty and Sheldon (1982b) found streamside philopatry to be common in their study of tailed frogs, commitment to a patch in the middle of a clear-cut seems unlikely unless some form of territoriality is occurring. High site fidelity is known to occur in adult amphibians (Martof 1953; Shoop 1968; Gill 1978a; Dingle 1980; Phillips and Sexton 1989; Berven and Grudzien 1990) and may serve a selective advantage in breeding success by decreasing exposure to negative factors such as predation and desiccation. This would be the case if the area of commitment serves a survival advantage. Patches may exist in clear-cuts that provide good cover or moister soils, but if overall mortality rates are higher, then such habitats could act as "sinks," and eventually lead to population declines despite its apparent attractiveness to *Ascaphus* (Gill 1978c; Doak 1995; Bryant 1998). It is difficult to address the reasons for this pattern due to the low numbers of recaptures. The recaptures do suggest however, that frogs are more active in mature

stands than in clear-cuts, or are surviving long enough in mature stands to encounter another trap during their movements.

Movement Direction and Distance to Streamside

Although there was no significantly preferred direction of movement in either of the habitats, some patterns were apparent. Frogs did not limit activities to within the immediate riparian zone (e.g., <5 m) and with the exception of immatures in clear-cuts, the proportion of captures generally decreased with distance from stream, similar to observations of other amphibians (e.g., Gomez 1992; McComb *et al.* 1993).

Movement parallel to the stream (upstream and downstream) was greater than movement perpendicular to the stream in both habitat types, similar to studies that tracked giant barred river frogs *Mixophyes iteratus* (Lemckert and Brassil 2000). While parallel movement was more than two times more frequent than perpendicular movement in clear-cuts in this study compared to mature stands, this may have been a reflection of the lower number of frogs captured in the mature stands. However, movement away from the stream made up the lowest proportion of captures in both clear-cuts and mature stands, which corresponded with the lowest numbers of frogs captured at the furthest distance (65 m) from the streams. The highest proportion of frogs moving upstream in mature stands supported Metter's (1964) conjecture that that *Ascaphus* may move upstream to headwater creeks for summer refuge. While water volume may be lower in these headwater streams, consistent, year-round water flow is more likely due to fewer human-induced impacts on hydrology (e.g., logging, development, agriculture), which increases at lower elevations. Higher elevation streams in the Chilliwack Valley are less

likely to be logged due to their relative inaccessibility and steep gradient. Moving upstream would decrease the probability of encountering a change in habitat quality resulting from such activities. The predominance of metamorphosed ASTR in small streams at higher elevations was also observed by Hunter (1998), who theorized that ASTR nests (egg masses) would be present in smaller streams that would have more stable substrate and reliable perennial flow. It may also be possible that ASTR shift their movement patterns seasonally along a resource gradient that was not detected within the time frame of this study.

While this study indicated that differences in patterns of movement existed between the two habitat types, drawing inferences based on the direction in which the frogs moved should be done with caution. The significant site variation revealed by the analysis for immatures was likely influenced by the high proportion of immatures caught in Tamihi, which comprised 90% of the total immature captures amongst all six study sites. A large, buffered S3/S5 stream (likely fish-bearing, 1.5 - 5 m)(Ministry of Forests 1995a; Stevens *et al.* 1995) was located less than 30 m downstream of the Tamihi grid. Upstream movement at this site would have involved traversing a logging road after approximately 100 m, followed by a steep escarpment another 50 m beyond, before reaching intact forest. This escarpment likely hindered upstream movement of tadpoles and metamorphs. The large number of tadpoles found in the small portion of the stream below the escarpment may be the only available habitat suitable for tadpole development, and productive enough to support a high density of tadpoles. Upon metamorphosis, frogs were likely moving downstream to the nearby large, buffered stream that was surrounded by intact forest. This habitat would provide more stable and favourable conditions than

moving upstream along a small, clear-cut stream prone to drying up (Landreth and Ferguson 1967). This may have been an influential factor behind the relatively higher number of immatures found moving downstream in clear-cuts, particularly Tamihi, in which the highest proportion of frogs (43%) moved downstream.

The low proportion of frogs caught moving away from streamside in both habitats may indicate that tailed frogs are conservative in their movements away from known sources of moisture (i.e., streams and riparian zones). *Ascaphus* orient towards water using both celestial and visual cues (Landreth and Ferguson 1967). However, this may only apply in undisturbed settings, as the distance data for CC indicated that more immatures were captured at the furthest distance from the stream. While high quality habitat may exist further from the stream in clear-cuts, it is also possible that new metamorphs are disoriented in CC, as was indicated by the higher number of CC frogs turning around and being recaptured in the nearest trap immediately upon being released.

As a dispersal mechanism, movement in juveniles may be selectively advantageous in securing food, shelter and favourable breeding grounds (Daugherty and Sheldon 1982b; Schwarzkopf and Alford 1999). If unoccupied patch habitats are available and mortality of migrating individuals is low, then juvenile dispersal will have high selective benefit, particularly if they are escaping degraded habitats, high density areas (Gill 1978b), or areas subjected to fragmentation (Berven and Grudzien 1990; deMaynadier and Hunter 1999). Future studies could evaluate rates of mortality for the various age classes within different habitats in order to evaluate long-term population trends for this species. Knowledge of both movement rates and habitat-specific

demographic rates are invaluable in determining the amount of habitat degradation a population can tolerate (Doak 1995).

Although Daugherty and Sheldon (1982b) found that *Ascaphus* movement activity did not vary with season, this study indicated that frog activity was greatest during the spring and fall months. Over the course of the trapping season, capture rates decreased substantially during the hot, dry months, then increased movement occurred with the onset of autumn and increasing precipitation. This is similar to the observations of (Noble and Putnam 1931), who found *Ascaphus* adults at greater distances from streams during the wet season and in higher abundances alongside streams during drier times, similar to that observed in *Rana clamitans* (Martof 1953). With little control over evaporative water loss (Zug 1993), amphibians tend to time their activities to coincide with that of favourable environmental conditions. While activity levels seemed to decrease during drier periods in this study, no significant patterns emerged with regards to these effects on frog proximity to streams. It may simply be that decreased activity resulted in a lower probability of being captured. *Ascaphus* have been found to move up to 4800 metres (3 miles) over an 11 week period in eastern Oregon (Landreth and Ferguson 1967), although no details were given on how this was measured. Otherwise, the most reasonably published maximum distance for *Ascaphus* movement has been 360 m over a 12.5 month period by an immature female (Daugherty and Sheldon 1982b). It is possible that the immatures in this study are also capable of such long distance dispersal under ideal landscape and/or environmental conditions, but survival probability may be reduced during movement through clear-cuts due to a greater vulnerability to desiccation resulting from a smaller body size (high surface:volume ratio) and semi-permeable skin

(Bellis 1962), particularly when exposed to increased sunlight and wind. Nocturnal movement would reduce these effects and/or movement only within the stream, which would not be detected by pitfall traps. However, more frogs should then have been observed during the evening surveys.

If habitat alteration makes seasonal variation more pronounced, then this may increase activity levels or create a greater need for habitat mosaics to deal with changing conditions (Law and Dickman 1998). While dispersal is theoretically favoured in variable habitats (McPeck and Holt 1992), studies have found that “wanderers” experience higher mortality rates than sedentary individuals due to the increased likelihood of encountering predators (Rappole *et al.* 1989). For smaller individuals (i.e., immatures), this would be combined with a greater susceptibility to desiccation. Thus, disturbances such as logging may lead to density dependent factors acting on immature survival that are otherwise not a problem under ideal conditions. Over time, gene flow may decrease if dispersal and colonisation rates are retarded in or due to clear-cuts (Berven and Grudzien 1990).

Apart from trap shyness (Sutherland 1996), two factors may explain the relatively low number of adult captures in clear-cuts: higher mortality resulting in fewer frogs surviving to adult stage, or movement out of the area to more favourable habitats. The greater number of adults caught relatively closer to streamside in the mature stands may suggest that philopatry serves an advantage under ideal conditions, but may shift if the habitat is altered (i.e., in clear-cuts).

For immatures, the greatest proportion of frogs was caught furthest from the streamside in clear-cuts, which supported the findings of (Daugherty and Sheldon 1982b)

that pre-reproductive *Ascaphus* move greater distances than adults. While immatures may have to move greater distances in clear-cuts to seek out appropriate habitat conducive to survival post-metamorphosis, territoriality may be another influential factor, but it is not known whether this occurs in *Ascaphus*. If territoriality does occur, it may act as a density-dependent mechanism that enhances fitness and survival (Wilbur 1980) particularly in degraded habitats if survival to adulthood is low. For example, territoriality may force young of the year (YOY) to immediately disperse upon metamorphosis, including into or through sub-optimal habitats such as clear-cuts. If territoriality exists in CC for what little suitable habitat is available, then it may explain the greater number of frogs being re-caught in the nearest trap immediately upon release.

Body measures and larval surveys

The high tadpole abundance in clear-cuts corresponds to the findings of Richardson and Neill (1998), who found *Ascaphus* tadpole densities to be higher in recently clear-cut streams than old growth streams, while average individual tadpole weights were lower. Although the overall analysis did not indicate a significant difference in weights between tadpoles in clear-cuts and those in mature stands, this may have been an artefact of the relatively low numbers of tadpoles used in the analysis for three of the sites (i.e., McTam, McGuire, Ford). Consequently, a biologically significant difference may have existed although the power of the analysis may have been unable to detect it (Cohen 1988; Peterman 1990; Thomas and Juanes 1996). Tadpoles from the Tamihi site, which comprised 93% of the clear-cut tadpole weights used in the analysis, were smaller than all other sites, and significantly smaller than the three mature sites. A

similar trend also existed with tadpole SVL and STL. The lack of any significant differences in these body measures may also have been confounded by the different age classes of tadpoles all being lumped together in the analysis. Multiple age cohorts of tadpoles are known to occur in streams (Daugherty and Sheldon 1982a; Brown 1990; Wahbe 1996), but were not assessed in this study.

The significant difference between clear-cuts and mature stands in the ratios of pitfall frogs to tadpoles in the corresponding stream indicates that some habitat effect may be occurring. The contrasting relationship between habitats may suggest a behavioural difference between habitats such that pitfall traps may be more efficient at sampling tailed frogs in one habitat over the other. However, it cannot be determined which proportion of the captures more reliably represented the true number of frogs within the habitat. It may also reflect a differential survival or emigration rate in either tadpoles or life stages post-metamorphosis between the two habitat types.

It is difficult to ascertain the reasons for the relatively abundant immatures in Tamihi. Tamihi was the oldest of the three CC sites, so stream productivity and established terrestrial vegetation may have contributed to enhanced habitat use (see Chapter 3 for analyses). Tamihi was also the highest elevation site, which also may have been a contributing factor (Welsh 1990; Bury *et al.* 1991a; Lemckert 1999). It has been suggested that productivity of stream ecosystems are enhanced due to greater light penetration and increased algal production immediately following logging (Murphy and Hall 1981; Hawkins *et al.* 1983; Hartman and Scrivener 1990; Richardson and Neill 1998). This being the case, then it is reasonable to deduce that high tadpole densities simply carried over into high metamorph densities. While habitat may be suitable for

tadpoles, it does not reflect suitability for other life stages (Van Horne 1983; Winker *et al.* 1995) and changes in survival rates over different age classes could make a difference between a population that is increasing or declining, similar to changes in birth rates (Hastings 1998). Even if habitat were suitable for all life stages, the current presence of a species may not be a good indicator of its future persistence (Lindenmayer 1995), as extinctions may occur over a prolonged period after disturbance (Tilman *et al.* 1994; Lindenmayer 1999). Breeding and recruitment may be successful in clear-cuts when conditions are favourable, but may lead to local extinction when conditions become unfavourable (Davis 1999). Conversely, if habitat suitability improves via succession over time, extinction might become less likely. Seburn *et al.* (1997) caution that large numbers of YOY in a site may be deceptive as not all YOY may originate from the same source. This suggests that dispersing YOY can make it appear that the site is successful when it in fact may not be. Ultimately, survival of individuals in a site is the best gauge of habitat suitability and its capacity (Winker *et al.* 1995).

For subadults and immatures, WT and SVL were lower in clear-cuts than in mature stands, as observed with the tadpole data. If productivity of CC streams is elevated and leads to an increase in tadpole development rate, then time spent in the larval habitat will be shorter, particularly if larval mortality rate is high, resulting in a smaller size at metamorphosis (Werner 1986). A smaller size however, may also make an amphibian more vulnerable to predation and desiccation, particularly in clear-cuts. While clear-cut streams may provide a favourable habitat for aquatic stages, the physiological needs of post-metamorphic stages shifts drastically. Clear-cut habitats with high terrestrial mortality may serve as population sinks, despite high densities of

immatures. Similar effects have been observed with other vertebrates (Gill 1978b; Doak 1995; Bryant 1998). Additionally, as canopy re-growth increases shade, negative effects of logging on ASTR may be masked by increased productivity (Richardson and Neill 1998). Thus tadpole densities in clear-cut streams would decrease over time with canopy regeneration and as density-dependent effects became more pronounced due to increased competition for resources. In the absence of long term monitoring, it can only be speculated as to whether lower tadpole densities will be counterbalanced by enhanced survival of metamorphs if terrestrial habitat becomes more suitable for survival with increasing canopy closure.

For disturbances such as clear-cuts, movements and life history strategies of newly metamorphosed individuals may differ in sensitivity relative to other age classes within the same species (deMaynadier and Hunter 1999). Numerous studies have documented a variety of mechanisms influencing anuran metamorphosis (e.g., Wilbur 1980; Skelly 1997; Bury and Adams 1999; Laurila and Kujasalo 1999). Isolating the most significant factors affecting *Ascaphus* metamorphosis in these sites would be extremely complex given the variation in environmental factors even amongst the sites in the same habitat type (clear-cut or mature). Plasticity amongst both larval and metamorph stages is well known in anurans (e.g., Wilbur 1980; Skelly 1997; Bury and Adams 1999; Laurila and Kujasalo 1999) and may be operating at a very fine, local scale resulting in the site variations observed. Although larvae may find refuge amongst subterranean moisture sources during drought, greater sensitivity to environmental cues may trigger rapid metamorphosis pre-drought within one year (Bury and Adams 1999).

General Study Considerations

Due to the low number of sites and the variation between the sites, this study had low statistical power to test many of the hypotheses (Peterman 1990). Thus interpretations should be made with caution. Both time and financial constraints limited the search for additional replicate sites given the landscape of the Chilliwack Valley, which resulted in the selection of the areas that were chosen.

With regards to making management decisions, taking action based on the rejection of the null hypothesis should only be done if the probability of making a Type II error is low. When dealing with conservation issues, it is more common to risk making a Type I error as a precautionary measure despite the risk of compromising “good” science and incurring great financial costs (McCoy 1994). The calculation of a detectable effect size is important when considering that a biologically or economically important effect might exist, although the experiment might have an unacceptably small chance of detecting it (Cohen 1988; Peterman 1990; Thomas and Juanes 1996). Additionally, biologically important differences will not necessarily reflect statistical significance if sample sizes are small (Johnson 1995). Likewise, finding a statistical difference does not always imply biological significance (Johnson 1999). Ideally, prospective (*a priori*) power analyses should be incorporated into the initial study design, or secondarily, retrospective (*a posteriori*) power analyses conducted after the fact (Steidl *et al.* 1997; Thomas 1997). Confidence interval estimation may also be used in lieu of retrospective power analysis (Steidl *et al.* 1997; Thomas 1997; Johnson 1999), although in this study, a small sample size would have resulted in a large overlap in standard errors and would not likely reflect any drastically different findings than that already observed (V. LeMay,

UBC, pers. comm.). Except in extreme cases, determining the level at which a decline is biologically significant cannot be achieved with complete confidence or agreement (Pechmann and Wilbur 1994; Thomas and Juanes 1996). This consideration should be kept in mind for future assessments of logging impacts on amphibian populations considering the economic and conservation implications of such management decisions.

While pitfall trapping is widely accepted as an effective means of sampling amphibians (e.g., Bury and Corn 1987; Corn and Bury 1990; Aubry and Hall 1991; Heyer *et al.* 1994; Gomez and Anthony 1996; Welsh and Hodgson 1997), biases are still inherent. Trap happiness or trap shyness may occur (Sutherland 1996), or habitat type may skew effectiveness towards a particular sex or age class (Block *et al.* 1998). It is also assumed that animals caught in traps are representative of those that are not caught, both in terms of fitness and behaviour. Throughout this study, two of the mature stands and two clear-cut sites were also used by researchers studying Pacific Giant Salamanders (*Dicamptodon tenebrosus*). It is possible that the additional activities of these researchers conducting stream surveys and radio telemetry in the sites may have influenced trappability due to increased habitat disturbance.

Due to BC Forestry regulations, glyphosate was aerially applied to the three clear-cut sites in September of 1998. While some herbicides are known to negatively impact amphibians (see Power *et al.* (1989) for a review), glyphosate has not been found to be severely detrimental (Berrill *et al.* 1997; Cole *et al.* 1997; Mann and Bidwell 1999). This was reflected in the continued trapping of animals in the months post-application.

Whether the vegetation that was cleared for transect surveys may have influenced behaviour and/or movement within the clear-cuts could not be assessed (see Chapter 3 for

detailed analyses). Severe microhabitat alteration also occurred during establishment of pitfall traps and drift fences, and quantitative assessment of any impacts this may have had on *Ascaphus* movement or habitat use is difficult to determine.

The scope of the study must be considered, and whether the scale used was appropriate to assess the effects being tested (Wiens *et al.* 1986). Forestry impacts can be measured at various scales (Bunnell and Huggard 1999), and while the scale used in this study was considered appropriate to assess movement and responses to habitat disturbance within these sites at the cutblock level (Bunnell *et al.* 1999), it was probably insufficient to reveal any larger scale population-level responses (deMaynadier and Hunter 1999). Seasonal shifts in activity and/or abundance did appear to be occurring in this study, but it is uncertain as to whether these shifts are infrequent or cyclic without long term monitoring.

Table 2.1. Locations and elevations for each of the six study sites within the Chilliwack Valley of southwestern British Columbia, Canada.

Clear-cut sites ¹	Age at time of grid set-up (yrs)	Lat/Long. ²	UTM ³	elevation ³ (metres)
Tamihi	4-5	N49°00.02'7"W121°45'7.9"	5428348N 591350E	680
McTam	3	N49°03'27.80"W121°48'25.00"	5434597N 587650E	580
McGuire	3	N49°03'43.6"W121°47'35.8"	5434969N 588400E	480
<u>Mature stands¹</u>				
Ford	141-250	N49°05'52.8"W121°35'45.9"	5439259N 602350E	500
Elk	81-100	N49°06'18.1"W121°49'06.80"	5439835N 586490E	680
Vedder	81-100	N49°04'04.1"W121°59'85.3"	5435508N 573150E	340

¹ At the time of the study, all clear-cut sites were <5 years old and mature stands >81 years

² Lat/long coordinates were acquired using a hand-held Garmin® GPS 38 Personal Navigator

³ UTM coordinates and elevations were visually derived from reading CFB Chilliwack Map MCE147 Ed. 3 (1:50 000) Series A702

Table 2.2. Total number of frogs caught in each age class per site and habitat type during the 1998-99 trapping season. These numbers represent pitfall captured frogs only.

Site Name	Age Class			
	adults	subadults	immatures	Site Total
Clear-cut sites				
McGuire	2	0	2	4
McTam	4	0	2	6
Tamihi	7	4	66	77
Clear-cut Total	13	4	70	87
Mature stands				
Elk	13	13	25	51
Ford	5	1	7	13
Vedder	8	3	13	24
Mature Total	26	17	45	88
Age Class Total	39	21	115	175

Table 2.3. Number of recaptures in each habitat type. Turnarounds are frogs that were recaptured in the nearest trap from which they were released within a 24 hour period.

	Mature Stands	Clear-cut sites	Total
Frogs previously caught in other trap stations	13	2	15
Turnarounds	1	5	6
Total	14	7	21

Table 2.4. P-values of $\ln(x+1)$ -transformed data for movement direction in each age class ($p < 0.05$). There were 3 sites within each habitat type (CC or M). Movement direction was upstream, downstream, towards or away from the stream.

Pitfall captures only	df	total frogs	adults	sub-adults	immatures
Habitat type	1	0.04	0.05	0.04	0.36
Direction	3	0.06	0.09	0.32	0.06
Direction x Habitat type	3	0.22	0.31	0.09	0.25
Site (Habitat type)	4	<0.01	0.09	0.02	<0.01
Error	12				

Table 2.5. P-values for site comparisons ($n = 15$ comparisons) based on the Least Square Means test for the effect of site nested within habitat type for the ANOVA on movement direction of immatures ($p < 0.003$). McGuire, McTam and Tamihi are clear-cut sites; Elk, Ford and Vedder are mature stands.

Site	McTam	Tamihi	Elk	Ford	Vedder
McGuire	1.00	<0.001	0.001	0.13	0.01
McTam	-	<0.001	0.001	0.13	0.01
Tamihi	-	-	0.01	<0.001	0.001
Elk	-	-	-	0.03	0.26
Ford	-	-	-	-	0.21

Table 2.6. Mean percentage of frogs caught in pitfall traps moving in each direction in each habitat type.

Movement Direction	clear-cuts	mature
away from stream	11	13
towards stream	21	32
downstream	34	15
upstream	34	40
Overall movement parallel to stream	68	55
Overall movement perpendicular to stream	32	45

Table 2.7. P-values of $\ln(x+1)$ -transformed data for distance from streamside in each age class ($p < 0.05$). There were 3 sites within each habitat type (CC or M). Capture distances from streamside were at 5 m, 25 m, 45 m, and 65 m.

Pitfall captures only	df	total frogs	adults	sub-adults ¹	immatures
Habitat type	1	0.09	0.03	0.18	0.22
Distance	1	0.12	0.56	0.99	0.11
Distance x Habitat type	1	0.35	0.19	0.67	0.20
Distance x Site (Habitat type)	4	0.30	0.10	0.81	0.03
Site (Habitat type)	4	0.04	0.18	0.53	0.01
Error	12				

¹Data were rank transformed to meet assumptions of normality.

Table 2.8. Mean body measures for frogs caught in pitfalls and during stream surveys at all sites. Numbers in brackets denote sample size. McGuire, McTam and Tamihi are clear-cut sites; Elk, Ford and Vedder are mature stands. Missing values reflect no captures or measures that were not obtained. Sex ratios were only determined for adults.

adults	WT (g)	SVL (cm)	STL (cm)	Total <i>n</i>	M:F:U
McGuire	5.68 (2)	3.81 (1)	4.44 (1)	2	1:0:1
McTam	7.13 (10)	4.15 (10)	4.62 (3)	10	7:3:0
Tamihi	7.18 (8)	4.20 (8)	4.44 (1)	8	3:4:1
Mean M:F Ratio					2:1
Elk	6.33 (19)	3.94 (19)	4.23 (5)	19	14:5:0
Ford	6.68 (5)	4.14 (5)	4.46 (3)	5	4:1:0
Vedder	7.81 (10)	4.21 (10)	4.51 (3)	10	6:4:0
Mean M:F Ratio					8:3
subadults	WT (g)	SVL (cm)	STL (cm)	Total <i>n</i>	
McGuire				0	
McTam				0	
Tamihi	2.15 (4)	2.47 (4)		4	
Elk	2.51 (14)	3.00 (14)	3.14 (10)	14	
Ford	2.65 (1)	3.02 (1)	3.30 (1)	1	
Vedder	2.41 (3)	2.75 (3)		3	
immatures	WT (g)	SVL (cm)	STL (cm)	Total <i>n</i>	
McGuire	1.26 (2)	2.42 (2)		2	
McTam	0.95 (4)	1.95 (4)	2.72 (2)	4	
Tamihi	0.96 (66)	2.15 (64)	2.70 (2)	66	
Elk	1.01 (26)	2.18 (26)		26	
Ford	1.49 (7)	2.54 (7)	2.91 (1)	7	
Vedder	0.82 (14)	1.93 (14)		14	

Table 2.9. Mean SVL, STL, and weights of tadpoles measured at each site. Units for SVL and STL are in cm, weights in grams. Numbers in brackets denote sample size. McGuire, McTam and Tamihi are clear-cut sites; Elk, Ford and Vedder are mature stands.

site	SVL	STL	Weight
McTam	1.40 (6)	4.25 (6)	0.88 (6)
McGuire	1.78 (2)	3.54 (5)	0.93 (3)
Tamihi	0.96 (127)	2.93 (127)	0.29 (127)
Ford	1.71 (1)	3.37 (8)	0.96 (1)
Elk	1.13 (44)	3.34 (44)	0.41 (44)
Vedder	1.19 (155)	3.43 (155)	0.49 (155)

Table 2.10. P-values for site comparisons ($n = 15$) based on the Least Square Means test comparing rank-transformed tadpole weights (g) in each site ($p < 0.003$). There were 3 sites within each habitat type (CC or M). McGuire, McTam and Tamihi are clear-cut sites; Elk, Ford and Vedder are mature stands.

Site	McTam	Tamihi	Elk	Ford	Vedder
McGuire	0.48	<0.001	0.10	0.36	0.28
McTam	-	<0.001	<0.001	0.61	0.01
Tamihi	-	-	<0.001	<0.003	<0.001
Elk	-	-	-	0.04	0.04
Ford	-	-	-	-	0.09

Table 2.11. P-values for site comparisons ($n = 15$) based on the Least Square Means test comparing rank-transformed tadpole SVL (cm) in each site ($p < 0.003$). There were 3 sites within each habitat type (CC or M). McGuire, McTam and Tamihi are clear-cut sites; Elk, Ford and Vedder are mature stands.

Site	McTam	Tamihi	Elk	Ford	Vedder
McGuire	0.12	<0.001	<0.001	0.97	0.004
McTam	-	<0.001	0.01	0.22	0.06
Tamihi	-	-	<0.001	<0.001	<0.001
Elk	-	-	-	0.01	0.02
Ford	-	-	-	-	0.04

Table 2.12. P-values for site comparisons ($n = 15$) based on the Least Square Means test comparing rank-transformed tadpole STL (cm) in each site ($p < 0.003$). McGuire, McTam and Tamihi are clear-cut sites; Elk, Ford and Vedder are mature stands.

Site	McTam	Tamihi	Elk	Ford	Vedder
McGuire	0.02	0.03	0.84	0.56	0.47
McTam	-	<0.001	<0.003	<0.003	0.01
Tamihi	-	-	<0.001	0.06	<0.001
Elk	-	-	-	0.27	0.17
Ford	-	-	-	-	0.07

Table 2.13. Total captures and ratios of tadpoles:metamorphosed frogs (all age classes combined) at each site. Frogs captured in both pitfall traps and during stream surveys are combined in the total metamorphs category. McGuire, McTam and Tamihi are clear-cut sites; Elk, Ford and Vedder are mature stands.

Site	Total Tadpoles	Total Metamorphs	Ratio
McGuire	5	4	1.25 : 1
McTam	6	14	0.43 : 1
Tamihi	127	78	1.63 : 1
Total CC	138	96	Mean: 1.1 : 1
Elk	44	59	0.75 : 1
Ford	8	13	0.62 : 1
Vedder	155	27	5.74 : 1
Total M	207	99	Mean: 2.4 : 1
Overall	345	195	

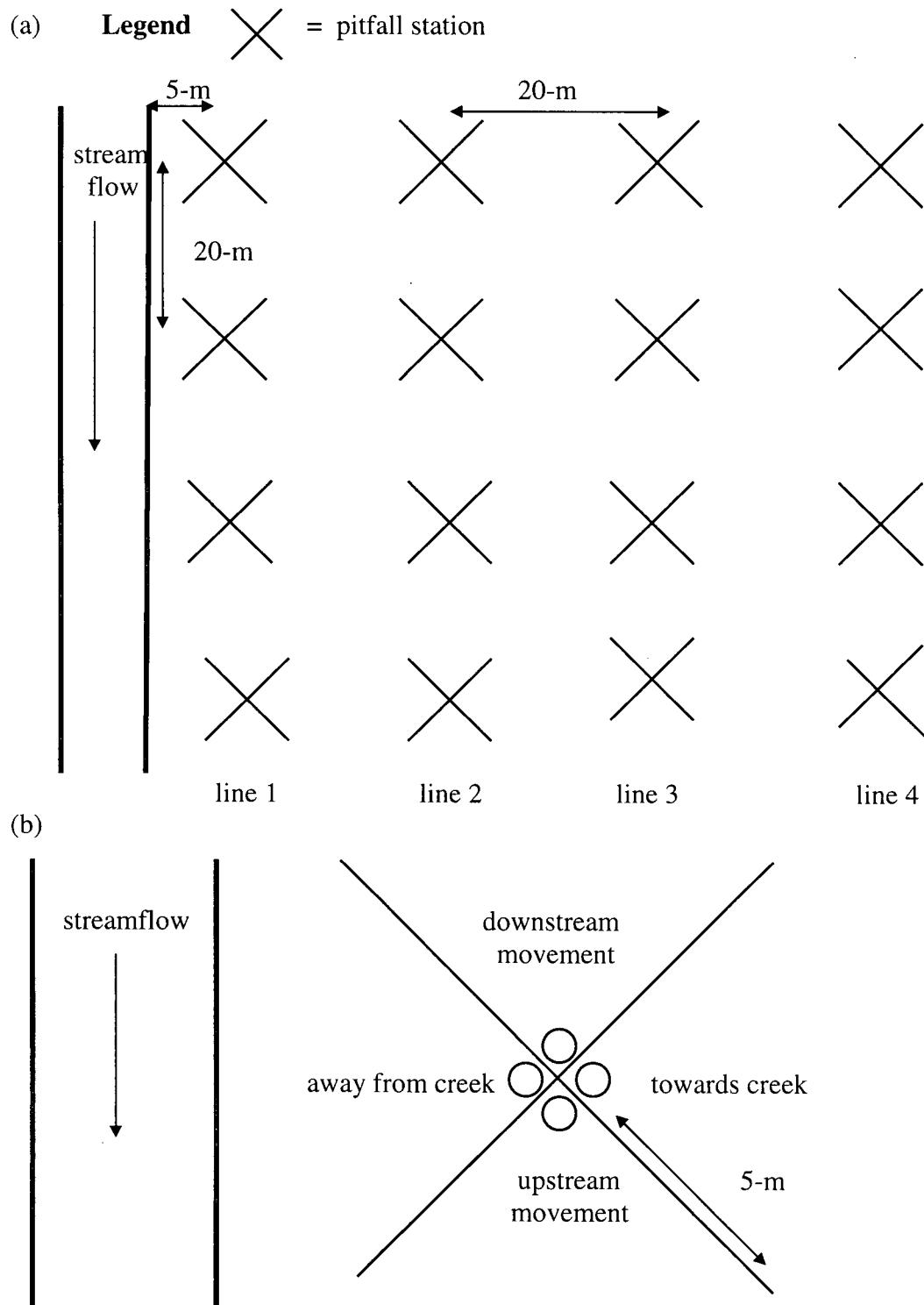


Figure 2.1. (a) Arrangement of pitfall trap stations in each study grid. "X's" indicate orientation of drift fences relative to streamflow. (b) Enlargement of a single pitfall station with a pitfall trap located in the centre of each crotch (four drift fences and four pitfall traps at each station). Trap position reflected the direction of movement by the frog.

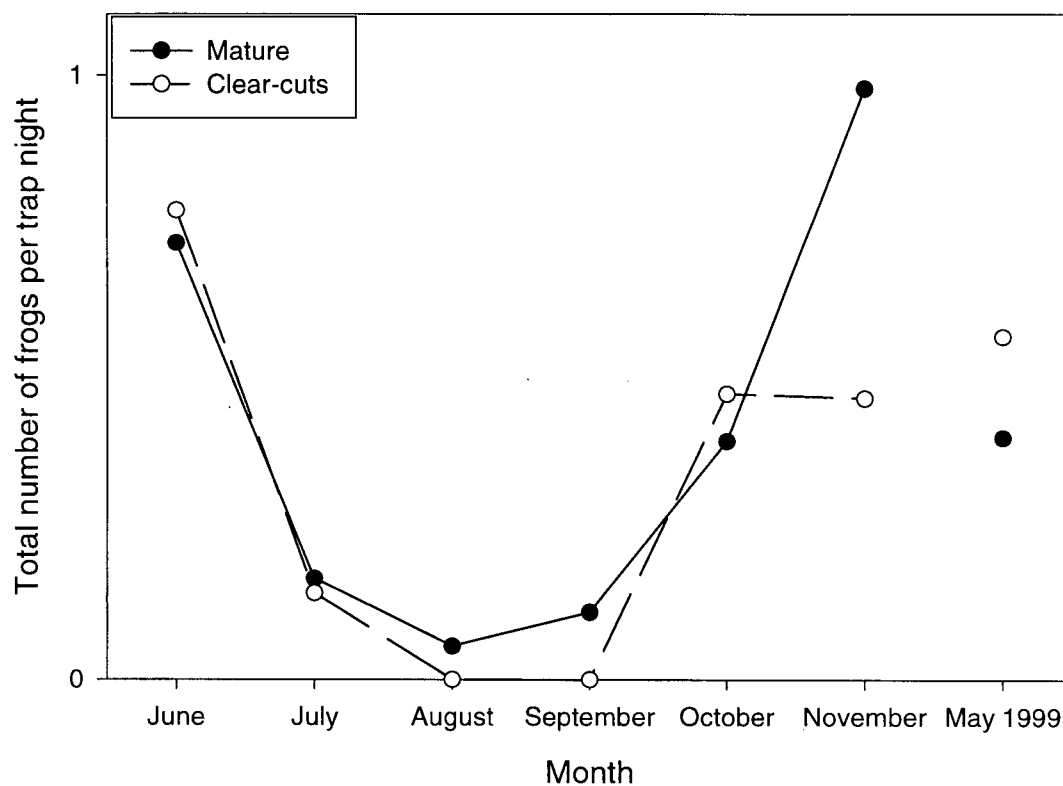


Fig. 2.2. Total number of frogs captured per trap night in each habitat type. All sites and ages within a habitat type are combined. Recaptures are not included. All captures were in 1998 (except for the May 1999 data). Captures for May 1998 are not shown as not all sites were operational at the time.

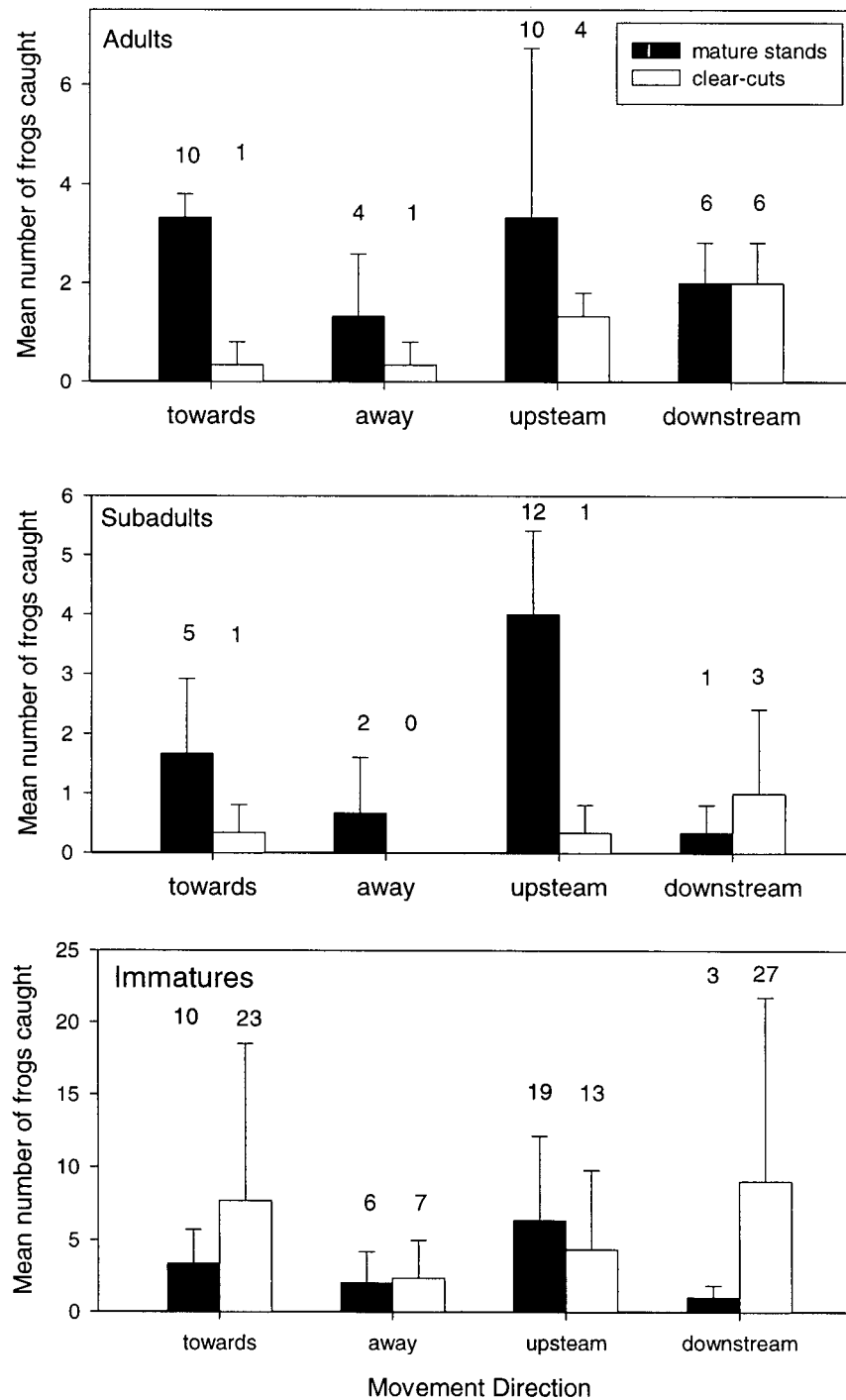


Fig. 2.3. Mean number of frogs per habitat type (and standard error) caught moving in each direction ($n = 3$ sites per habitat type). Numbers above bars indicate n used to determine means.

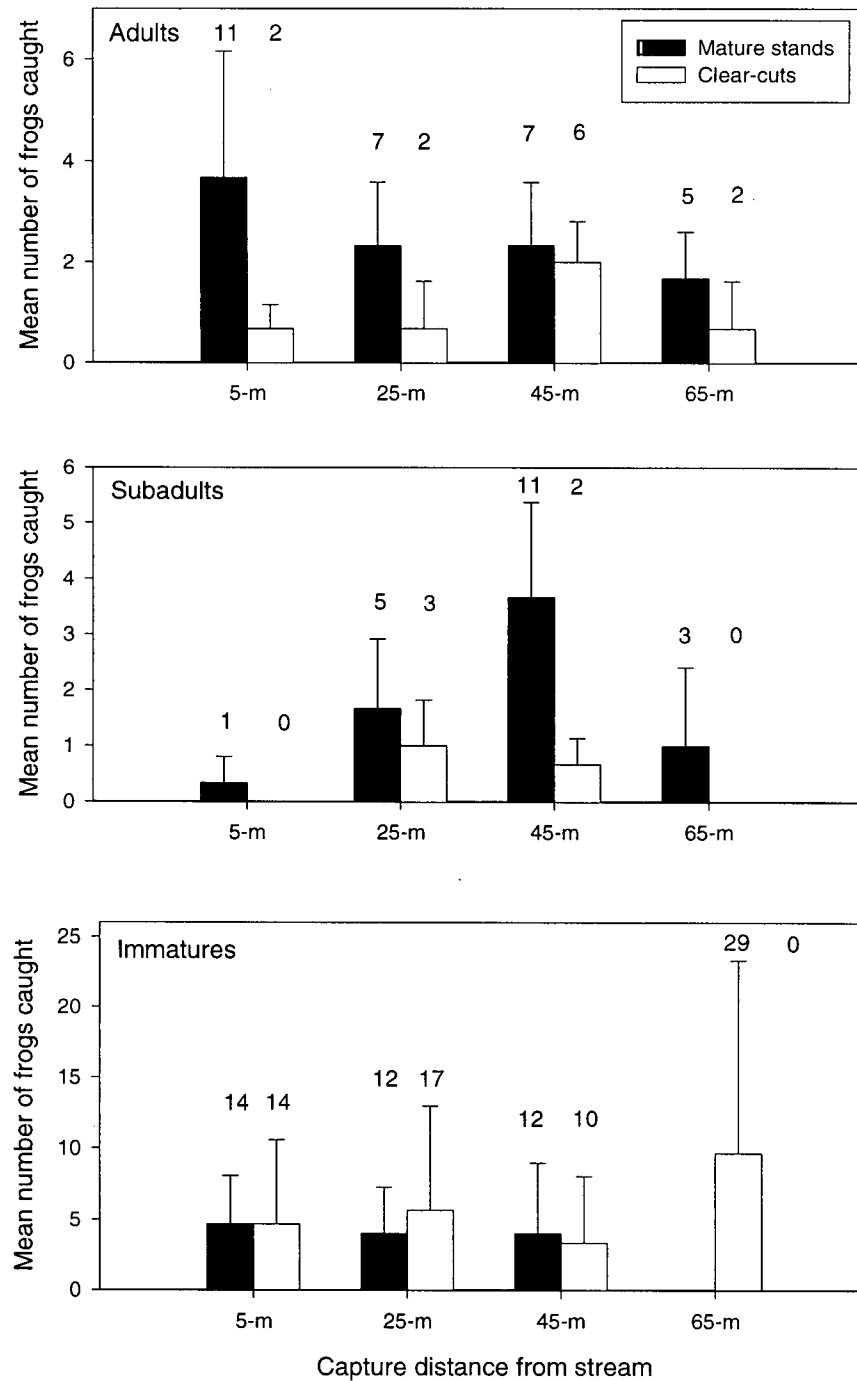


Fig. 2.4. Mean number of frogs per habitat type (and standard error) caught at each distance from the stream ($n = 3$ sites per habitat type). Numbers above bars indicate n used to determine means.

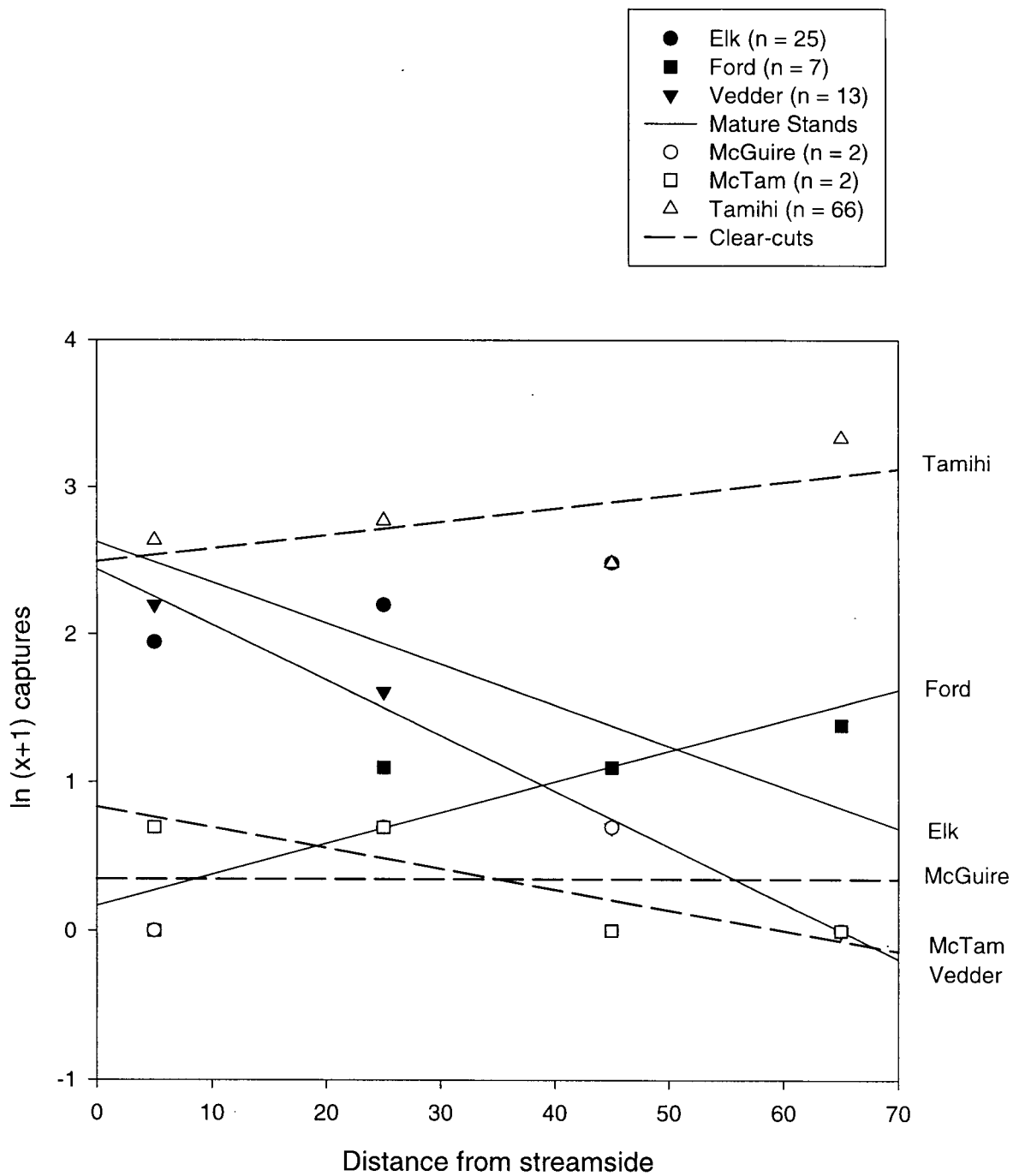


Fig. 2.5. Captures of immature tailed frogs ($\ln(x+1)$ -transformed) and corresponding regressions relative to distance from streamside for each site.

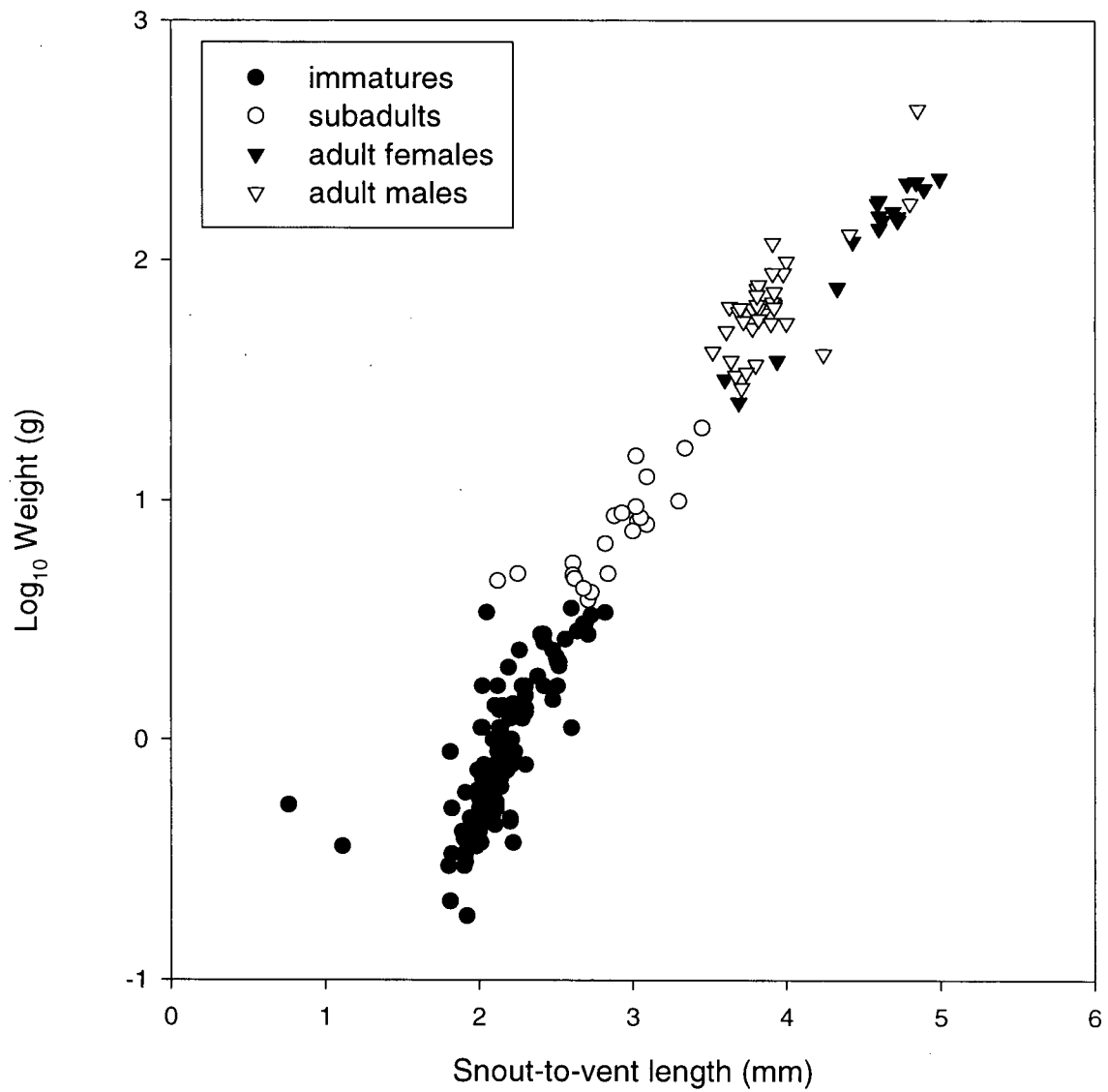


Fig. 2.6. Log₁₀ weight (g) and snout-to-vent length (mm) for all metamorphosed tailed frogs caught in pitfall traps and during creek surveys. Both clear-cut and mature captures are combined.

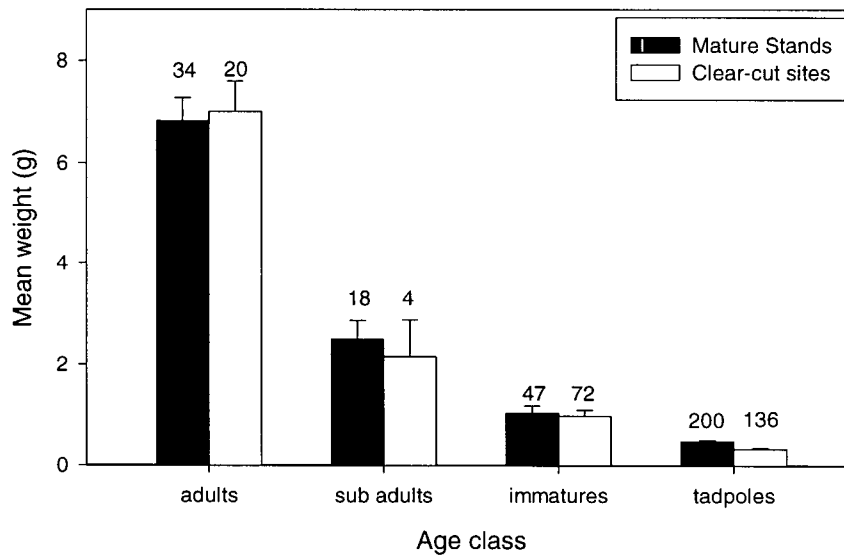


Fig. 2.7. Mean weight (g) and standard error for each age class. All sites were combined in each habitat type. Frogs from both pitfall captures and stream surveys were used to determine means. Numbers above bars indicate n used to determine means.

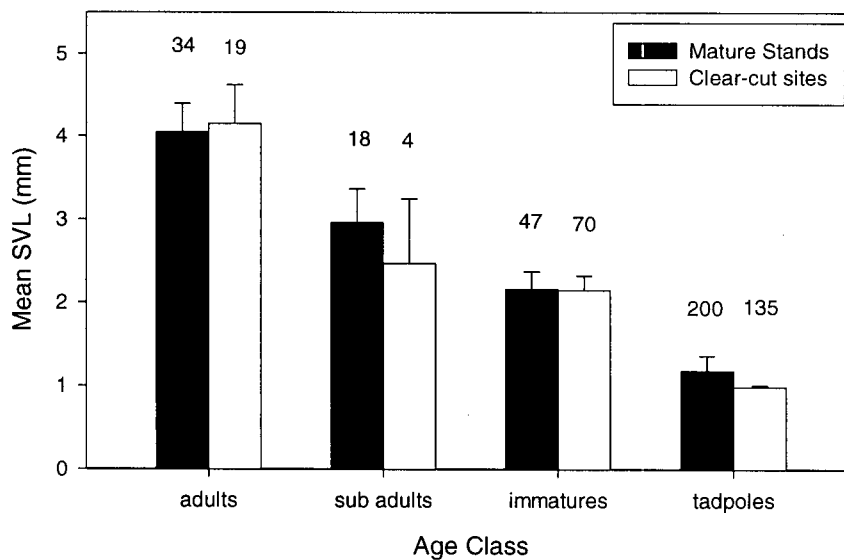


Fig. 2.8. Mean SVL (mm) and standard error for each age class. All sites were combined in each habitat type. Frogs from both pitfall captures and stream surveys were used to determine means. Numbers above bars indicate n used to determine means.

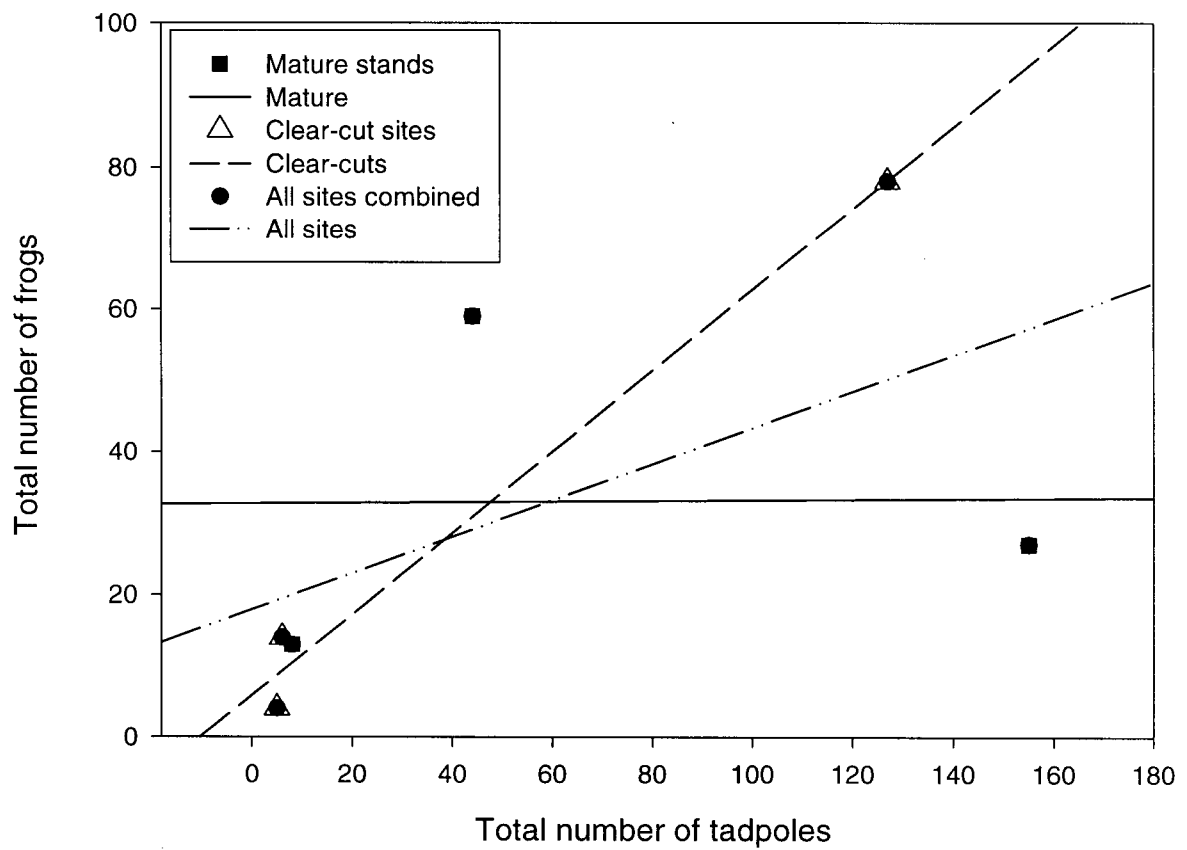


Figure 2.9. Regressions for the ratios of total metamorphosed frogs relative to the number of tadpoles found in the corresponding stream for each habitat type and over all habitats combined.

Chapter 3. Habitat associations of tailed frogs in clear-cuts and mature forest stands

Introduction

The effective management of a species and/or its habitat requires an understanding of their interrelationships and that of other components tied to their sustainability. When a habitat is altered, any effects on populations or species of concern must be assessed and, if warranted, steps taken to mitigate possible adverse impacts. Although attempts are made to mimic natural disturbance regimes, logging activities may alter landscapes on a scale more cyclic than that of natural causes, with impacts that persist within the ecosystem long after harvesting activity has ceased.

In British Columbia (BC), timber harvesting effects on wildlife are a politically and economically charged issue. Most research on the habitat relationships of terrestrial vertebrates associated with BC forests has focused on birds (e.g., Wetmore *et al.* 1985; Schwab and Sinclair 1994; Easton and Martin 1998) and mammals (e.g., Archibald *et al.* 1987; Nyberg *et al.* 1989; Kremsater and Bunnell 1992). While studies are increasing on species that are less visible and currently considered economically unimportant (e.g., amphibians, reptiles), there is still a paucity of information about the extent of such relationships with forests in BC. This information is vital to our understanding of ecosystem processes. As a presumed associate of old growth and mature forests, the tailed frog (*Ascaphus truei*) is becoming increasingly used as a means of assessing logging impacts on amphibians. However, studies to date in BC have predominantly focused on habitat attributes associated with larval stages (e.g., Wahbe 1996; Richardson and Neill 1998; Dupuis and Steventon 1999). Most of the

information on habitat associations with post-metamorphic terrestrial stages has come from studies conducted in the Pacific northwestern United States (e.g., Daugherty and Sheldon 1982b; Welsh 1990; Aubry and Hall 1991; Bury *et al.* 1991a), often gathered during research focused on other vertebrates. While structurally similar to forests elsewhere within the Pacific northwest, forest microhabitats in BC may differ as a result of latitudinal differences (i.e., species being at their northern range limits) and the physical and biological diversity of landscapes (Ministry of Forests 1994). As such, population dynamics of tailed frogs in Canada may vary from that observed in more southern, warmer climates (e.g., via delayed metamorphosis; Bury and Adams 1999).

As habitat quality is a measure of an area's contribution to individual fitness and population persistence (Van Horne 1983), knowledge of habitat associations with resident populations allows for effective management decisions to be made that contributes to ecosystem functioning and maintenance. Habitat conditions are often used as indices of population status (Morrison *et al.* 1992; Block and Brennan 1993), the validity of which relies on the relationships between habitat characteristics and the population parameter being assessed (Block *et al.* 1998).

The objective of this study was to determine if features exist that significantly influence use of habitat by tailed frogs. Assessing the extent of associations between tailed frog abundance and characteristics of its surrounding habitat may help explain the patterns of movement observed in Chapter 2, and provides insight on ways to sustainably manage populations in conjunction with timber harvesting.

Methods

For details on study site set-up, see the Study Site and Methods sections of Chapter 2 [pg.12], Table 2.1 [pg.38] and Figure 2.1 [pg.44].

Field Measures of Environmental Variables

At each of the 16 pitfall stations in each study site, the percentage cover of each plant species, leaf litter (leafy material, needles, twigs/sticks < 5 cm diameter), standing water/mud, running water, exposed bare ground, and rocks, was estimated visually at each station within a 7 m diameter circular plot centred over each pitfall station. A larger ring with an 11.2 m diameter was centred around each pitfall station using nine sequentially numbered wooden stakes. One of the stakes was randomly chosen (using a random numbers table) to place a small, 2 m diameter circular plot centred on the stake, to estimate the percentage of mosses, lichens, and fungi present at the station. Mosses, lichens and fungi were not identified to species, but classified as belonging to one of these three groupings. The 11.2 m diameter plot covered an area of 0.01 ha and facilitated easier assessment of cumulative measures of basal area for stumps, snags, and trees at each site for later comparison. Diameter was measured for all stumps, and basal area (from diameter at breast height; 1.3 m above ground) measured for all snags and live trees ≥ 5 cm diameter occurring within each 11.2 m diameter plot.

The percentage of overhead canopy closure was measured by eye from each of the nine numbered stakes and from the centre of the trap station, by looking directly overhead through a 40 cm length of 2 cm diameter PVC piping. Relative canopy closure for the station was then calculated as a proportion of the ten visual points based

on whether foliage was in view (open) or partial or complete foliage was seen through the pipe (closed)(Wind 1996).

For each station, coarse woody debris volume was measured using a 10 m transect (Marshall *et al.* 2000) that extended outwards from one of the numbered stakes (chosen using a random numbers table), in a randomly chosen direction. Diameter was measured for all downed woody debris (DWD) material ≥ 5 cm (i.e., downed branches, logs) at the point of intersection with the transect line, also noting whether the piece was perpendicular to the transect line (Marshall *et al.* 2000). The angle of each piece relative to the horizontal plane was measured using a Suunto[®] clinometer. For all logs, trees, snags or stumps, diameters to a maximum of 90 cm were measured using folding calipers; diameters greater than this were calculated by measuring circumference with a measuring tape. To reduce observer bias, relative decay classes for each piece of woody material was determined by holding a 20 cm long, Gerber[®] river knife 20 cm directly above the DWD piece, and allowing it to drop into the piece (for guidance, the knife was held alongside the 40 cm PVC pipe used for the ocular estimation). Increments (1 cm) were marked on the knife blade, with relative decay class indicated by the depth to which the knife stuck into the DWD piece ($0 < 1$ cm = no decay = decay class 1, $1 \geq 2$ cm = decay class 2, $2 \geq 3$ cm = decay class 3, etc. up to a decay class of 7+, which was considered to be extremely decayed/soft). For other site-specific details, see Chapter 2, Table 2.1 [pg.38], and Appendix 1 [pg.99].

Due to the length of time required to measure these variables, vegetation estimates and coarse woody material measures were only conducted once during the

study period in July/August 1998, while frog capture rates were low enough to allow sufficient time to conduct these measures at each of the trap stations.

Attempts were made to assess relative soil moisture in each site by use of various moisture meters but were eventually abandoned due to inaccuracy and unreliability of the gauges, and loss/damage of meters presumably as a result of animal tampering. Soil moisture, nutrient quality and climatic categorisation of sites was assessed *post-hoc* using the VTab Ecosystem Reporter Program (VTab 1999). This program assigns quantitative scores to the plots (stations) based on the percentage of indicator plant species estimated at the station, and was originally designed for comparing relative measures of habitat quality for sites in BC. The premise underlying the use of plants as site indicators is based on the predictive capacity of the plant to assess habitat quality when the occurrence and vigour of the plant is known (Klinka *et al.* 1989). These values are derived measures based on the relative percent frequency of each indicator plant species present and produces scores that can be used to compare relative measures between sites. It also provides a consistent evaluation of site attributes that may greatly fluctuate when measured over short periods of time and/or may require repeated or numerous measurements (e.g., soil moisture regime; Klinka *et al.* 1989).

For soil moisture, derived measures were used from four out of six specified categories, as there were no indicator plants representative of the two extremes in the moisture gradient, excessive to very dry, and wet to very wet. The four categories compared were, along a gradient of increasing moisture, very to moderately dry

(VMD), moderately dry to fresh (MDF), fresh to very moist (FVM), and very moist to wet (VMW).

Soil nutrient regime can be correlated with vegetation and forest productivity, and is an index of the average amount of soil nutrients available to vascular plants (Klinka *et al.* 1989). As nitrogen is one of the most important factors limiting plant growth (Ballard and Carter 1986), the soil nutrient regime delineates three categories, nutrient poor (NP), nutrient medium (NM), and nutrient rich (NR), along major segments of the available soil nutrient gradient (Klinka *et al.* 1989).

For climatic assessment of the sites, five out of six categories produced scores based on the indicator plant species present: tundra and boreal (TB), subalpine boreal and cool mesothermal (SBCM), montane boreal and cool temperate (MBCT), cool mesothermal (CM), cool temperate and mesothermal (CTM). The cool temperate and semi-arid category was not used in the comparison as none of the plant species in any of the sites were representative of this category. Climatic variation between the sites was thus evaluated by comparing indicator plant species cover within these climatic categories. These categories represent a wide and overlapping portion of the climatic gradient, but can be used to make inferences on regional climates, local climates, and microclimates (Klinka *et al.* 1989). While regional climate may fluctuate due to variation of local topography and canopy cover, the main reason for climatic assessment in this study was to assess site variations in microclimate, which may affect distribution, abundance and activities of amphibians.

Data Analysis

All analyses were conducted using SAS (1994) with significance levels set at $\alpha = 0.05$. For each pitfall station, a total of 116 habitat variables were assessed, of which 90 were estimates of percentage of plant species cover at the station (see Appendix 3 [pg.101]). Plant species coverage estimated at less than 0.5% within the station was assigned a value of 0 and assumed to have no influence on the data analysis. Other habitat attributes associated with each pitfall station that were estimated included: percentage of the station area covered by bryophytes (BRY), lichen (LICH), fungi (FUNG), bare ground (BAGRD), leaf litter (LL), rocks (ROCK), standing water (STDH2O) or running water (RUNH2O), overhead canopy closure (CAN), volume of DWD decay class 1 (DC1), volume of DWD decay class 2 (DC2), etc. up to DC7, total volume of DWD (all decay classes combined), volume of stumps (STP), volume of DWD + STP combined (DWDSTP), basal area of conifers (BACON), basal area of deciduous trees (BADEC), total basal area of live trees (TOTBALV), total basal area of snags and stumps (SNGSTP), and total basal area for live and dead trees combined (BALVDD)(see Appendix 3 [pg.101] for site means).

The number of habitat variables was reduced prior to any multivariate analyses to obtain an adequate sample size to variable ratio (Williams *et al.* 1990) and decrease sources of error. Based on the percentage of coverage estimated at each station for the ninety plant species, only the top 15 species occurring in at least three sites and having a cumulative total of 60% or greater across all six sites were used in further analyses. Thus, a total of 36 habitat variables (15 plant species estimates and 21 other variables) were initially used in the analyses (Appendix 3) [pg.101].

A principal components analysis (PCA) was used to identify groupings of variables among the pitfall trap grids. The PCA transformed the set of correlated variables into uncorrelated variables (principal components) using the Pearson correlation matrix to determine which principal components best explained the greatest proportion of variability amongst the sites (Beauregard and Leclair 1988). The first few principal components extract the most variance (Tabachnick and Fidell 1996), so only the first three components were used in further analyses. The most influential variables on the principal component scores were then plotted to illustrate their relative distribution within the ordination space (Porter *et al.* 1998). Frog abundance was plotted against Axis 1 to illustrate any patterns between the variables and principal component 1. Spearman correlation was used (due to the non-normal distribution of frog data) to determine the extent of the relationship between age classes and the habitat variables. Sixteen relatively significant habitat variables were chosen from the Spearman correlation and entered into a Canonical Correlation Analysis to confirm any patterns arising from the PCA. Similar to the PCA, component scores were plotted to illustrate their relative distribution within the ordination space.

The 16 habitat variables were then entered into a discriminant analysis (DFA)(class = site) using Pearson Correlation to predict the site(s) based on the variables that were used. The DFA assigned similarity scores to the sites by comparing each site with each other, allowing a generalised assessment of reliability of site classification. This was confirmed by an output indicating the number and percentage of correctly classified stations in each site relative to the other sites.

Variables that consistently and significantly delineated sites were plotted against frog abundance to reveal any patterns. If a site consistently stood out as being distinct amongst the other sites within the same habitat type, the data for the site was excluded and the graph re-plotted to assess the influence that site variation might have had on the initial analysis.

For soil moisture, nutrient regime and climatic categorisation, derived measures for the percent relative frequency of plants in each category could not be analysed statistically, but provided comparisons to determine the extent of the relationship between each site and the category being assessed.

Results

The PCA delineated the sites into two groups based on the habitat attributes measured at each pitfall station with 11 relatively strong habitat correlations indicated (Table 3.1) [pg.72]. Lichen, fungi, and DWD decay classes 5-7 were not used in the analyses as they occurred infrequently and thus were not expected to have a significant impact on tailed frog habitat use. Examination of the groupings arising from the PCA indicated that the habitat variables used in the analysis were typically characteristic of either clear-cuts (e.g., thimbleberry, Douglas fir seedlings, BASTP) or mature stands (e.g., leaf litter, CAN, TOTBALV; Table 3.1) [pg.72]. The two habitat types were strongly separated along Principal Component Axis 1 (Figure 3.1) [pg.77], which accounted for 24% of the variation amongst the sites (Table 3.1) [pg.72]. Axis 1 had relatively significant positive correlations with thimbleberry (THBE), Douglas fir seedlings (DOFI), BASTP, and SNGSTP, and negative correlations with CAN, LL,

BACON, and TOTBALV (Table 3.1) [pg.72]. Thus, large positive values along Axis 1 indicated sites high in THBE and DOFI, basal area of stumps and snags, with low amounts of overhead canopy, leaf litter, conifers and live trees (i.e., clear-cuts)(Figure 3.1a) [pg.77]. There were fewer significant correlations along Axis 2, which was positively correlated with DC2, DWD, and DWDSTP (Table 3.1) [pg.72]. There were relatively weaker correlations along Axis 3, but the Tamihi site separated along this axis (Figure 3.1b) [pg.77], which explained 7% of the variation and was characterized by relatively strong positive correlations with fireweed (FIWE; $r = 0.59, p < 0.0001$), foamflower (FOFL; $r = 0.53, p < 0.0001$), and BALVDD ($r = 0.62, p < 0.0001$), and negatively correlated with red elderberry (REEL; $r = -0.44, p < 0.0001$). This indicated that Tamihi had higher amounts of FIWE, FOFL, and BALVDD than any other site, and the lowest amount of REEL.

Using Spearman Correlation, the 16 most strongly correlated variables were selected from the 36 variables originally entered in the analysis ($p < 0.05$) for each of the frog age classes. The overall total number of frogs had relatively strong correlations with decreasing vine maple (VIMA), horsetail (HORS), willowherb (WIHE), thistle (THIS), and BRY. Adults were correlated with higher amounts of LL and CAN and with decreasing THBE, salmonberry (SABE), REEL and THIS. More subadults were correlated with higher CAN and RUNH2O, and decreasing THIS, STP, BASTP and SNGSTP. Immatures tended to increase with greater amounts of FIWE and FOFL, and decreasing VIMA and THIS. Total frogs and immatures had a relatively strong positive correlation with PC3 (Table 3.2) [pg.73].

When the number of frogs was plotted along Axis 1, there was a slight increase in the number of total frogs and immatures, although adults reflected a slight decrease (Figures 3.2a and b) [pg.78]. When data for the Tamihi site was removed and the points re-plotted, these trends reversed, with total frogs and immatures decreasing along Axis 1, and the decreasing adults became more pronounced along Axis 1 (Figures 3.2c and d) [pg.78]. Thus, the total number of frogs increased along Axis 1 with increasing DOFI, THBE, BASTP and SNGSTP, and decreased with CAN, LL, BACON and TOTBALV (Figure 3.2a) [pg.78], but when the Tamihi data was excluded, this trend reversed (Figure 3.2c) [pg.78]. Similar patterns were revealed when significant habitat variables were plotted against frog numbers with and without the Tamihi data. Leaf litter was consistently revealed by analyses to delineate sites, so when this variable was plotted against frog numbers, a decreasing trend for total numbers and immatures was indicated as percentage of LL increased, although adult numbers increased slightly (Figures 3.3a and b) [pg.79]. When Tamihi data was excluded, all age classes of frogs increased (Figures 3.3c and d) [pg.79]. When frog numbers were plotted against foamflower however, the trend was less marked. While total frogs and immature numbers increased with increasing foamflower and adults appeared unaffected (Figures 3.4a and b) [pg.80], exclusion of Tamihi data resulted in the increasing trend becoming less pronounced, although adult numbers reflected a decrease as foamflower increased (Figures 3.4c and d) [pg.80].

The canonical discriminant analysis supported the findings of the PCA. Relatively strong, positive correlations (≥ 0.70) along Axis 1 occurred with THBE, BASTP, and SNGSTP, and negative correlations with CAN and LL (Table 3.3)

[pg.74]. Axis 2 delineated the Tamihi stations amongst the clear-cuts, as FIWE and FOFL increased (Figure 3.5a) [pg.81], similar to that of the PCA analysis (Table 3.1) [pg.72]. While correlations were relatively weaker along Axis 3, the McGuire site separated as HORS, SABE and WIHE increased, and the McTam site separated as THBE decreased (Figure 3.5b) [pg.81].

The DFA indicated that these 16 habitat variables were relatively sufficient in predicting group membership by site, although only 50% of the Elk pitfall trap stations were correctly classified and 56% of the Ford stations (Table 3.4) [pg.75]. While the clear-cut sites were clearly distinct from the mature sites based on these habitat attributes, Tamihi also had relatively high dissimilarity scores (pairwise generalised squared distance) with the other two clear-cut sites (Table 3.5) [pg.75]. All mature stands were similar in habitat attributes. Pearson correlation analysis confirmed that post-disturbance, early successional plant species were significantly correlated with clear-cuts, particularly in Tamihi (FIWE, FOFL), McGuire (HORS), and McTam (WIHE)(Table 3.6 [pg.76]; also see Appendix 3 [pg.101]). Amongst the mature stands, CAN and LL generally had high, positive correlations. With the exception of LL in Elk, this simply indicated that there was more canopy closure and leaf litter in mature stands (Table 3.6) [pg.76].

From the VTab scores, the total percent frequency of indicator plant species at each station revealed that the McGuire clear-cut had a relatively high proportion of plants indicating very moist to wet conditions (Table 3.7a) [pg.76]. Thus, plant composition indicated that the McGuire site was the moistest of the study sites, which corresponded to the continual groundwater flooding of many of the McGuire pitfall

traps throughout the duration of the study. Based on indicator plants, Elk scored second highest in soil moisture and had the highest moisture scores among the mature sites. While Tamihi scored lowest among the clear-cuts, Ford scored substantially lowest over all the sites, indicating that it was the driest of the study sites (Table 3.7a) [pg.76].

For soil nutrient regime, indicator plant frequency suggested that the Vedder mature site had the most nutrient-rich soil, followed by McGuire, which scored highest among the clear-cuts (Table 3.7b) [pg.76]. While Vedder scored highest over all the sites for plants indicating nutrient-rich conditions, scores for the clear-cut sites were consistently higher than mature stands, which had greater fluctuation in scores within this category (Table 3.7b) [pg.76].

For climatic categories, the VTab derived measures from the indicator plant comparisons delineated the Tamihi clear-cut with the highest score in the cool temperate and mesothermal category, followed by Elk among the mature sites (Table 3.7c) [pg.76]. However, the range of variation was more consistent in the cool mesothermal category, particularly among the mature sites. Within this category, the Vedder and Ford sites scored highest followed by the McGuire clear-cut (Table 3.7c) [pg.76].

To summarise the comparisons of the VTab scores, McGuire was moistest and one of the most nutrient-rich sites; Tamihi had the most plants indicative of cool temperate and mesothermal climates; and Ford was exceptionally dry overall. All other sites fell somewhere within a gradient of these categories.

Discussion

The multitude of analyses conducted on the habitat variables indicated that differences existed between sites in attributes such as plant species composition, volume of downed woody debris, and basal area of trees and stumps. Soil moisture and nutrient regime are linked to many of these processes, and the VTab analyses revealed that these factors also varied by site. Numerous other factors that were not evaluated (e.g., elevation, slope, aspect) will also influence habitat attributes, but the overall analyses revealed that site variation existed and may have some bearing on the abundance and activity levels of frogs in the sites.

There were clearly significant differences in habitat attributes associated with the sites within the two habitat groupings (clear-cut or mature), thus analysis based on these groupings was justified and directly comparable as distinct habitat types. Future studies could focus on similar methods of analysing habitat attributes and associations with frog (or other animal) abundance, with emphasis on *a priori* efforts to seek out sites as similar as possible within habitat type. This will reduce site variability within habitat type, and facilitates easier interpretation of analyses directly to the influences that these attributes may have on animal abundance and activity levels.

The number of variables measured at the sites were reduced prior to analyses to reduce error by keeping the sample-variable ratio low (Williams *et al.* 1990). However, selection of which variables to exclude is important as variable elimination may not change the magnitude of the first correlations, but may increase the probability of attributing correlations to population-wide sources of covariation, rather than situation-specific covariance (Thorndike 1978). Although reduction of variables may eliminate

variables behaving independently of the patterns under examination, caution is heeded as the corresponding coefficients may also vary (Cassie 1969). In extreme cases, exclusion of the wrong variables may alter the scope of the study (Karr and James 1975). Conversely, care must also be taken not to combine variables that have no apparent relation (Smith 1981). In this study, out of the 116 variables measured at each station, it was subjective and difficult to tease apart the less important variables in the analysis as all likely have some relationship with one another. This selection was based on the assumption that those variables with low weighting (e.g., minimal amount of coverage by the plant), had little effect on tailed frog abundance. However, it is possible that there may have been indirect effects that were not detected in the analysis.

While relatively significant correlations with habitat variables arose out of these analyses, interpretations should be made with caution. For example, the analysis indicated that frog numbers increased with foamflower, but this was likely a result of high capture rates coinciding with the site that was also high in foamflower (i.e., Tamihi; see Chapter 2), and does not necessarily imply a causal mechanism. Due to the significant site variation resulting from the Tamihi CC, concluding that foamflower may be favoured by immatures may be presumptuous. The more plausible explanation is that more immatures are associated with clear-cuts, which also happens to be high in foamflower. Since foamflower was quantitatively most abundant in Tamihi, along with captures of immatures, the correlations may be spurious. This was supported by the finding that frog abundance changed when the Tamihi data was excluded from the analysis of leaf litter and foamflower and plotted the significant variables along Axis 1. Immatures made up the greatest bulk of captures (66% over all six sites; see Table 2.2

[pg.39]), and any correlations with immatures in the analysis would likely influence the outcome of the analysis on overall frog numbers, as was indicated by the similar regressions between total frogs and immatures when plotted against leaf litter and foamflower.

Similarly, the number of adults positively correlated with habitat attributes typical of clear-cuts and negatively correlated with attributes typifying mature stands suggested that adults are associated with mature forest habitat attributes, supporting the findings from Chapter 2. Thimbleberry, leaf litter, etc., may have some effect on abundance, but it would be hasty to isolate these variables as factors regulating abundance, as correlation does not imply causal mechanisms. Future studies assessing habitat requirements of metamorphosed tailed frogs can verify if these patterns are consistent, but it is recommended that efforts be directed towards assessing physiographic influences such as elevation, aspect, and slope, and variables such as precipitation, wind direction and cloud cover, with regards to population responses of tailed frog specifically within BC.

Structure of vegetation may be a more important factor in habitat selection than specific species composition (MacArthur and MacArthur 1961; Beauregard and Leclair 1988), but was not thoroughly assessed in this study. While correlations between vegetation variables and tailed frog abundance have not been detected in previous studies (Metter 1964; Bury *et al.* 1991a; Gilbert and Allwine 1991), biologically meaningful associations may still be present between data sets that have no statistically significant correlations (Blackith and Reyment 1971). When analysed separately, specific variables may have strong associations with abundance, but such patterns may

be masked or overwhelmed during group analysis of variables. Even when detected, patterns are difficult to interpret for amphibians, leaving habitat values open to speculation (Aubry and Hall 1991).

Due to sampling constraints, vegetation was only evaluated once at each site, even though vegetation composition, density and structure change seasonally. Thus the possibility exists that correlations between vegetation and frog abundance may also shift as vegetation patterns change. While visual estimation is sufficient for providing relative estimates of plant cover (Aubry and Hall 1991), the method is subjective and prone to bias depending on the plant identification and estimation skills of the observer.

Soil moisture has been found to be a major limiting factor of anuran distributions in terrestrial habitats (Roberts and Lewin 1979), particularly preference for moister habitats (Heatwole 1982), but was not found to be an important factor for tailed frogs in this study. Fewer frogs were caught in the driest site (Ford) and the wettest site (McGuire)(Appendix 2 [pg.100]), compared to findings that more tailed frogs occurred in dry sites than in moist sites in Oregon (Gilbert and Allwine 1991). The sites with the majority of captures, which also represented both habitat types, Elk (M) and Tamihi (CC), were most strongly correlated with the intermediate zone of the moisture gradient, suggesting that there may be thresholds beyond which tailed frog abundance may be affected by soil moisture conditions at either end of the moisture gradient.

The lack of correlations between frog numbers and soil nutrient regime and plants indicative of various climate habitats suggest that neither of these variables had any bearing on frog abundance in this study. However, these factors will affect

vegetation structure, and this must be kept in mind in future studies assessing relationships between tailed frogs and vegetation patterns. Similarly, no correlations were revealed with downed woody debris volume, in contrast to studies stressing the importance of these materials to amphibians, particularly lungless salamanders (see deMaynadier and Hunter (1995) for an overview). However, the large variation in DWD volume measured from the individual pieces within the 10 m transect line, may have been an insufficient length to adequately sample DWD volume at each pitfall station (V. LeMay, UBC, pers. com.). Downed woody debris does significantly contribute to forest habitats (Maser *et al.* 1988), and will have direct bearing on microhabitats, which may affect amphibian populations (deMaynadier and Hunter 1995). While frogs may utilise such cover objects for periods of time (e.g., overwintering, predator avoidance or minimising desiccation), this could not be evaluated with the sampling methods used in this study.

Several other habitat factors differed between sites analysed statistically, and may have influenced tailed frog abundance patterns. Tailed frog abundance is more closely associated with physiographic variables such as elevation, slope and aspect rather than vegetative features (Welsh 1990; Bury *et al.* 1991a). The Tamihi site, which had the highest captures, was also one of the highest elevation sites (see Table 2.1) [pg.38] and the only CC with a south-facing aspect (Appendix 1) [pg.99]. Both these features have been correlated with higher abundances of tailed frogs (Bury *et al.* 1991a). Various factors associated with these physiographic variables such as air temperature, stream temperature, relative air and soil humidity, and wind strength may also affect habitat use, but could not be reliably measured in this study.

Studies in the tropics have found that numbers of amphibian species generally decline with increasing altitude and dryness (Scott 1976; Heatwole 1982). If a similar pattern exists in temperate regions, then this may be the reason for tailed frogs being the only amphibian captured in the Tamihi clear-cut (Appendix 2) [pg.100], which was also the highest elevation site. Western toads (*Bufo boreas*) and Pacific giant salamanders (*Dicamptodon tenebrosus*) also occur at this elevation, but were not captured in Tamihi pitfall traps. This may reflect niche specialization of tailed frogs to exploit high altitude areas that other amphibians are incapable of utilizing if habitat has been disturbed such as alteration resulting from logging, or may indicate behavioural shifts in other amphibians such that they are less likely to be captured by pitfall traps.

The high abundance of immatures does not imply that populations would be able to persist over time, but may reflect conditions currently conducive to immature activity, and provides no indication of survival, reproductive success or long-term habitat suitability (Van Horne 1983; Saunders *et al.* 1991). As the Tamihi captures were mainly YOY (i.e., immatures), it is possible that these numbers reflected seasonal pulses of new emergers, or dispersers moving through the site, and may be a misleading indicator of abundance patterns and habitat requirements (Bury *et al.* 1991a; Gilbert and Allwine 1991). High densities of YOY do not imply that a population is successfully breeding, although large numbers dispersing over a wide area may give that appearance (Seburn *et al.* 1997). Even if the population is successfully breeding in the interim, there is no implicit expectation that the population would continue to do so should conditions become unfavourable (Davis 1999). In some cases, social interactions may prevent individuals such as sub-dominant immatures, from entering

high quality habitat. Immatures may then be forced to utilise low quality habitats, where densities may widely fluctuate (Lidicker 1975) and they are more vulnerable to environmental stochasticity, particularly in disturbed habitats. These low quality habitats may act as “sinks” where animals survive and/or reproduce poorly. As there is nothing to prevent sub-dominant individuals from entering low quality sink habitats, densities may at times exceed that of adult-dominated high quality or source habitats (Van Horne 1983). Fretwell and Lucas (1969) theorised that if densities are high in good quality habitat, the per-individual probability of success for unestablished immigrants (i.e., newly metamorphosed YOY) may be higher in poor quality than good quality habitat as they face a higher probability of failure to reproduce successfully and a greater mortality in good quality habitats as unestablished immigrants. Thus it may be individually advantageous for them to remain in the lower quality habitat. Alternatively, situations may occur where surviving young move back into high quality “adult” areas once they reach sexual maturity (Bradshaw 1971). Territoriality or hierarchical structuring is not known to occur in tailed frog populations, but it has not been thoroughly investigated, and provides food-for-thought with regards to the high numbers of immatures in the Tamihi clear-cut.

Table 3.1. Pearson correlation coefficients and corresponding probabilities ($p < 0.05$) for the habitat variables with the relatively strongest correlations along the first three principal components axes over all six sites. Units for volume are in m³/ha and area in m²/ha.

(a) Percentage of total variance ¹ explained by each component		24%		9%		7%	
Variable	Code	PRIN1	p	PRIN2	p	PRIN3	p
thimbleberry <i>Rubus parviflorus</i>	THBE	0.71	<0.0001	-0.10	0.33	-0.26	0.01
Douglas fir seedling <i>Pseudotsuga menziesii</i>	DOFI	0.75	<0.0001	-0.10	0.32	0.12	0.25
decay class 2 down woody debris volume	DC2	-0.15	0.14	0.85	0.00	-0.11	0.29
overhead canopy closure	CAN	-0.96	<0.0001	0.07	0.52	0.13	0.20
downed woody debris volume	DWD	-0.18	0.09	0.94	<0.0001	-0.11	0.30
total volume (dwd + stumps)	DWDSTP	-0.02	0.86	0.97	<0.0001	-0.04	0.68
basal area: conifers	BACON	-0.74	<0.0001	-0.15	0.14	0.26	0.01
basal area: stumps	BASTP	0.82	<0.0001	0.15	0.14	0.43	<0.0001
total basal area live trees	TOTBALV	-0.81	<0.0001	-0.15	0.15	0.24	0.02
total dead basal area (snags + stumps)	SNGSTP	0.81	<0.0001	0.19	0.06	0.43	<0.0001
leaf litter	LL	-0.82	<0.0001	0.06	0.57	0.16	0.13

¹ Variance based on scaled variables from the correlation matrix.

Table 3.2. Spearman correlation coefficients and corresponding probabilities ($p < 0.05$) for the first 3 principal components and the 16 habitat variables strongly correlated with each of the frog age classes.

Variable	Code	total			sub-			p	immatures	p
		frogs	adults	p	adults	p	immatures			
Principal Component 1	Prin1	0.01	-0.11	0.96	-0.20	0.05	0.14	0.19		
Principal Component 2	Prin2	0.15	0.01	0.14	0.09	0.40	0.21	0.04		
Principal Component 3	Prin3	0.30	0.22	<0.01	-0.01	0.96	0.27	0.01		
thimbleberry <i>Rubus parviflorus</i>	THBE	-0.21	-0.28	0.04	-0.21	0.04	-0.09	0.38		
red elderberry <i>Sambucus racemosa</i>	REEL	-0.19	-0.28	0.06	-0.24	0.02	-0.06	0.58		
fireweed <i>Epilobium angustifolium</i>	FIWE	0.17	-0.11	0.10	-0.17	0.10	0.31	<0.01		
foamflower <i>Tiarella trifoliata</i>	FOFL	0.35	-0.05	<0.01	0.05	0.62	0.48	<0.01		
horsetail <i>Equisetum</i> sp.	HORS	-0.30	-0.20	<0.01	-0.10	0.35	-0.24	0.02		
salmonberry <i>Rubus spectabilis</i>	SABE	-0.02	-0.26	0.81	-0.16	0.12	0.13	0.20		
thistle <i>Cirsium</i> sp.	THIS	-0.42	-0.34	<0.01	-0.29	<0.01	-0.32	<0.01		
vine maple <i>Acer circinatum</i>	VIMA	-0.27	-0.07	0.01	-0.10	0.32	-0.31	<0.01		
willowherb <i>Epilobium</i> sp.	WIHE	-0.26	-0.24	0.01	-0.22	0.03	-0.18	0.08		
bryophytes	BRY	-0.25	-0.15	0.01	-0.11	0.26	-0.15	0.15		
running water	RUNH2O	0.14	0.16	0.16	0.27	0.01	0.04	0.69		
basal area: stumps (m ² /ha)	STP	-0.18	-0.15	0.08	-0.32	<0.01	-0.07	0.51		
basal area: stumps (m ² /ha)	BASTP	-0.14	-0.18	0.17	-0.33	<0.01	0	0.97		
total dead basal area (snags + stumps) (m ² /ha)	SNGSTP	-0.09	-0.18	0.36	-0.27	0.01	0.06	0.53		
leaf litter	LL	0.11	0.26	0.29	0.19	0.07	-0.04	0.72		
overhead canopy closure	CAN	0.13	0.25	0.22	0.25	0.01	-0.02	0.87		

Table 3.3. Correlations between habitat variables and their canonical variables for the first three canonical axes over all six sites. '*' denotes relative significance ≥ 0.70 for Axis 1 (CAN1) and Axis 2 (CAN2), and relative significance ≥ 0.30 for Axis 3 (CAN3). Units for volume are in m^3/ha and area in m^2/ha .

Variable	Code	CAN1	CAN2	CAN3
thimbleberry <i>Rubus parviflorus</i>	THBE	0.71*	0.27	-0.16
fireweed <i>Epilobium angustifolium</i>	FIWE	0.47	-0.75*	0.08
foamflower <i>Tiarella trifoliata</i>	FOFL	0.44	-0.76*	0.01
horsetail <i>Equisetum</i> sp.	HORS	0.28	0.37	0.62*
salmonberry <i>Rubus spectabilis</i>	SABE	0.25	0.16	0.33*
willowherb <i>Epilobium</i> sp.	WIHE	0.54	0.41	0.46*
overhead canopy closure	CAN	-0.99*	-0.08	-0.002
basal area: stumps	BASTP	0.70*	-0.13	0.08
total dead basal area (snags + stumps)	SNGSTP	0.67	-0.13	0.08
leaf litter	LL	-0.85*	-0.08	-0.004

Table 3.4. Percentage and (number) of the 16 pitfall stations in each site correctly classified by discriminant analysis based on the habitat variables. Elk, Ford and Vedder are mature stands; McGuire, McTam and Tamihi are clear-cut sites.

Site	Elk	Ford	Vedder	McGuire	McTam	Tamihi
Elk	50 (8)	25 (4)	25 (4)	-	-	-
Ford	13 (2)	56 (9)	31 (5)	-	-	-
Vedder	12 (2)	0	88 (14)	-	-	-
McGuire	-	-	-	88 (14)	12 (2)	0
McTam	-	-	-	6 (1)	94 (15)	0
Tamihi	-	-	-	0	0	100 (16)

Table 3.5. Dissimilarity values based on pairwise generalised squared distances between sites for the 10 most significant habitat variables determined by the discriminant analysis. Elk, Ford and Vedder are mature stands; McGuire, McTam and Tamihi are clear-cut sites.

Site	Elk	Ford	Vedder	McGuire	McTam	Tamihi
Elk	0	-	-	-	-	-
Ford	4.40	0	-	-	-	-
Vedder	3.78	5.67	0	-	-	-
McGuire	344.38	367.67	328.34	0	-	-
McTam	347.36	372.25	331.12	23.16	0	-
Tamihi	424.40	452.22	411.88	48.10	46.24	0

Table 3.6. Pearson correlation coefficients and corresponding probabilities of habitat variables revealed by the discriminant analysis as being most strongly correlated with each site within habitat type ($p < 0.05$). Elk, Ford and Vedder are mature stands; McGuire, McTam and Tamihi are clear-cut sites.

Mature Sites						
Variable	Ford	p	Vedder	p	Elk	p
canopy closure	0.59	<0.0001	0.60	<0.0001	0.63	<0.0001
leaf litter	0.59	<0.0001	0.57	<0.0001	0.38	0.0001
bryophytes	0.75	<0.0001	-0.22	0.03	0.11	0.30
Clear-cut Sites						
	McTam	p	McGuire	p	Tamihi	p
fireweed	-0.16	0.11	-0.10	0.33	0.82	<0.0001
foamflower	-0.14	0.18	-0.16	0.13	0.81	<0.0001
willowherb	0.71	<0.0001	0.11	0.28	-0.05	0.62
horsetail	-0.13	0.21	0.70	<0.0001	-0.14	0.18

Table 3.7 Percent relative cover of each indicator plant species assessed by Vtab (1999) in each site for (a) moisture categories, (b) soil nutrient regimes, and (c) climatic categories, as outlined by Klinka *et al.* (1989). Categories which had no plant species representative within the site are not shown. Elk, Ford and Vedder are mature stands; McGuire, McTam and Tamihi are clear-cut sites.

(a) Moisture	Elk	Ford	Vedder	McGuire	McTam	Tamihi
Very to moderately dry	0.79	0.40	0	0.17	0.31	0.11
Moderately dry - fresh	11.07	25.10	0.64	5.14	4.96	4.75
Fresh - very moist	44.66	73.97	68.84	45.95	58.45	68.40
Very moist - wet	43.48	0.53	30.52	48.74	36.28	26.74

(b) Soil Nutrient Regime						
Nutrient-poor	3.59	4.82	0.09	0.75	0.79	5.73
Nutrient-medium	9.33	19.61	4.32	5.59	6.29	3.62
Nutrient-rich	87.08	75.56	95.59	93.66	92.92	90.64

(c) Climatic Categories						
Tundra and boreal	0	0	0	0.13	0	0.28
Subalpine boreal and cool mesothermal	1.85	0.61	0.47	0.13	1.98	0.55
Montane boreal and cool temperate	1.11	0.00	0.12	0.13	3.56	15.03
Cool mesothermal	71.59	88.84	98.60	85.62	75.10	22.76
Cool temperate and mesothermal	25.46	10.54	0.82	13.99	19.37	61.38

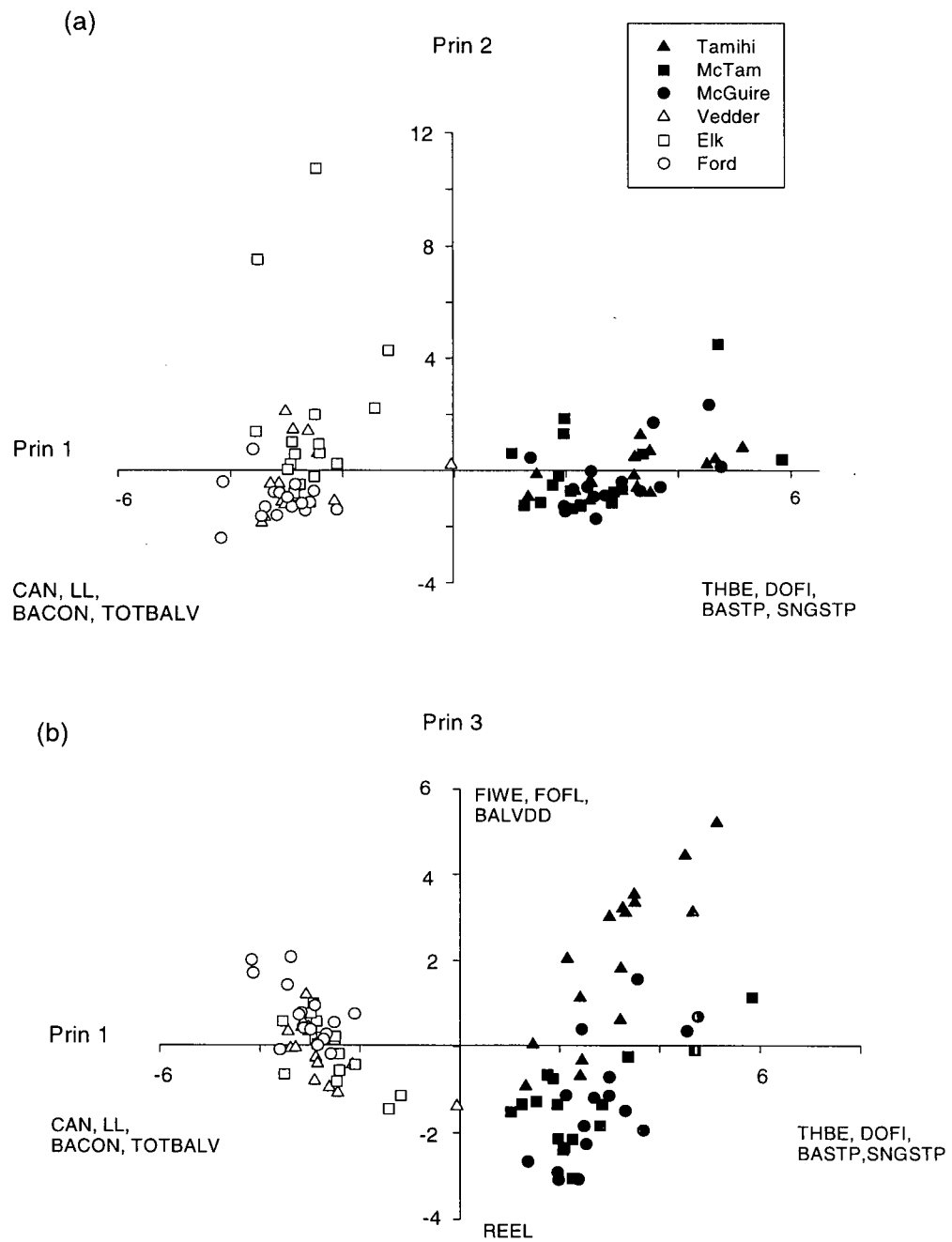


Fig. 3.1. Principal components analysis of the 36 habitat variables used to separate the six study sites. Tamihi, McTam and McGuire are clear-cut sites; Vedder, Elk and Ford are mature stands. Habitat variables that strongly separated sites are indicated along their respective axes. (a) Habitat variables separated along Axis 1 (Prin 1) and Axis 2 (Prin 2), and (b) along Axis 1 and Axis 3 (Prin 3).

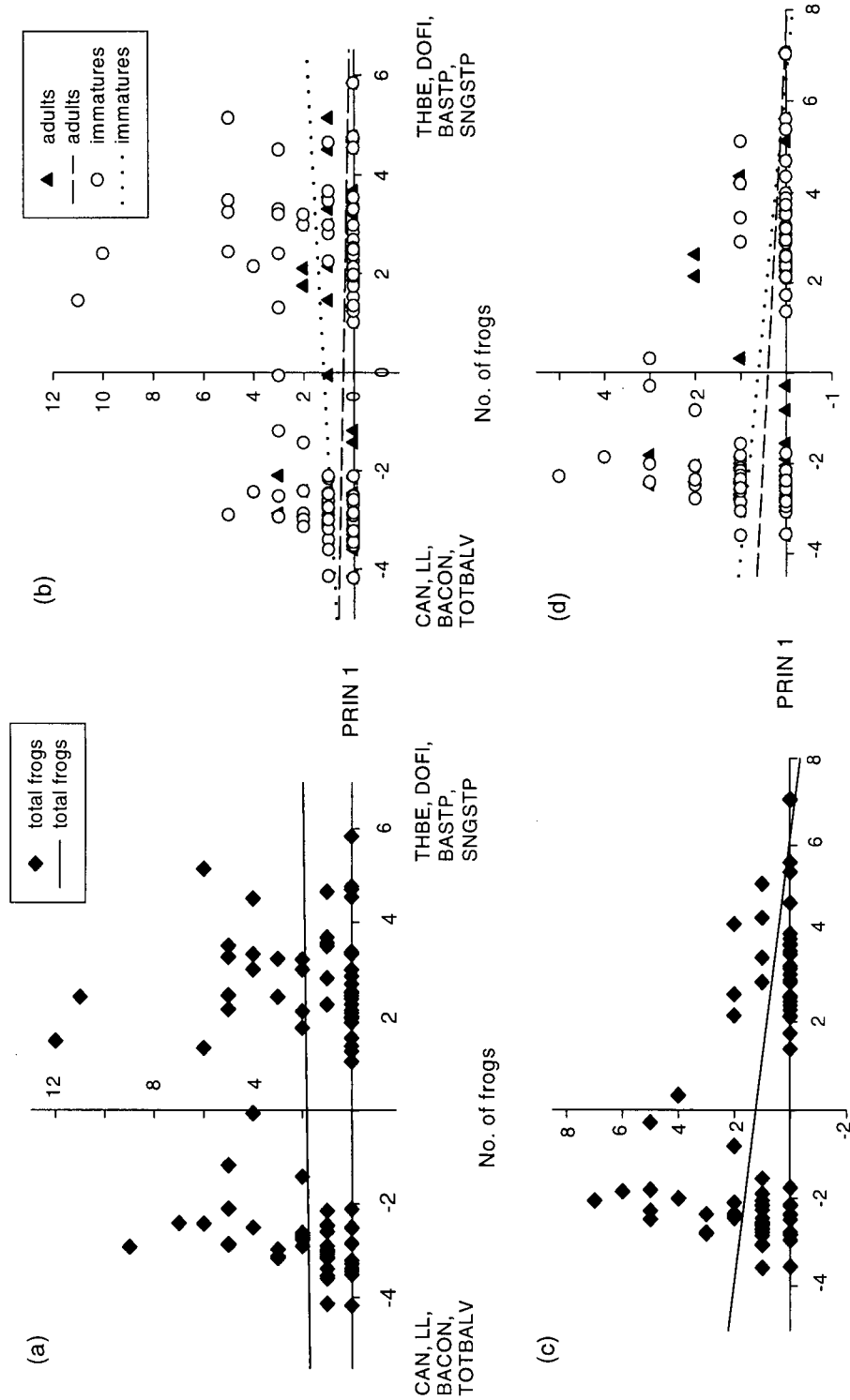


Figure 3.2. Frog numbers and corresponding regressions plotted against principal component 1 (PRIN 1) for (a) total frogs (all ages combined) and (b) adults and immatures. Due to the variation resulting from the Tamih site, Tamih data was removed and the points re-plotted for (c) total frogs (all ages combined) and (d) for adults and immatures. Habitat variables that strongly separated sites are indicated along axis 1.

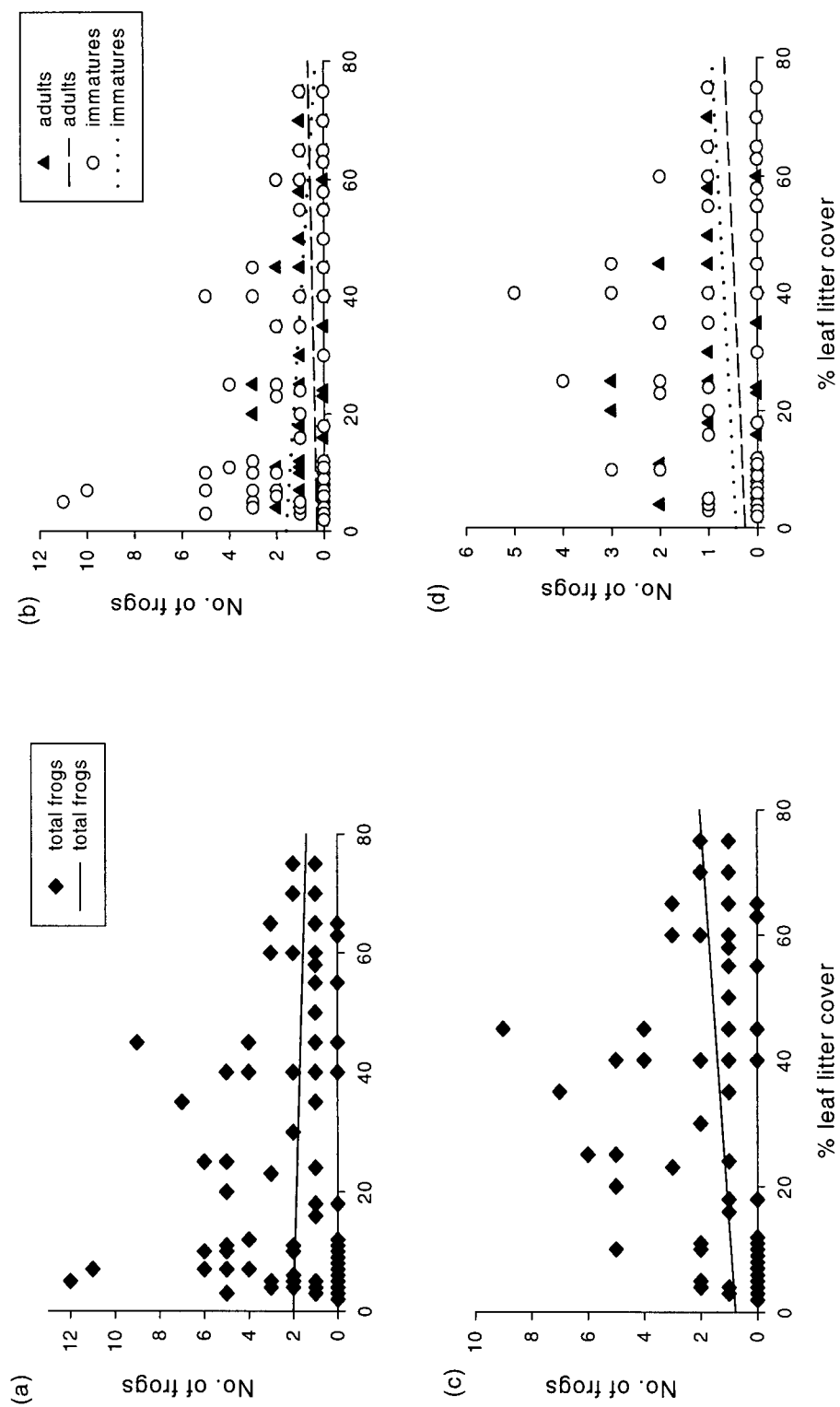


Figure 3.3. Frog numbers and corresponding regressions plotted for estimated percentage of leaf litter at each pitfall station and (a) total frogs (all ages combined) and (b) adults and immatures. Due to the influence of the high number of Tamihi clear-cut captures, points were re-plotted excluding the Tamihi data for (c) total frogs (all ages) and (d) adults and immatures.

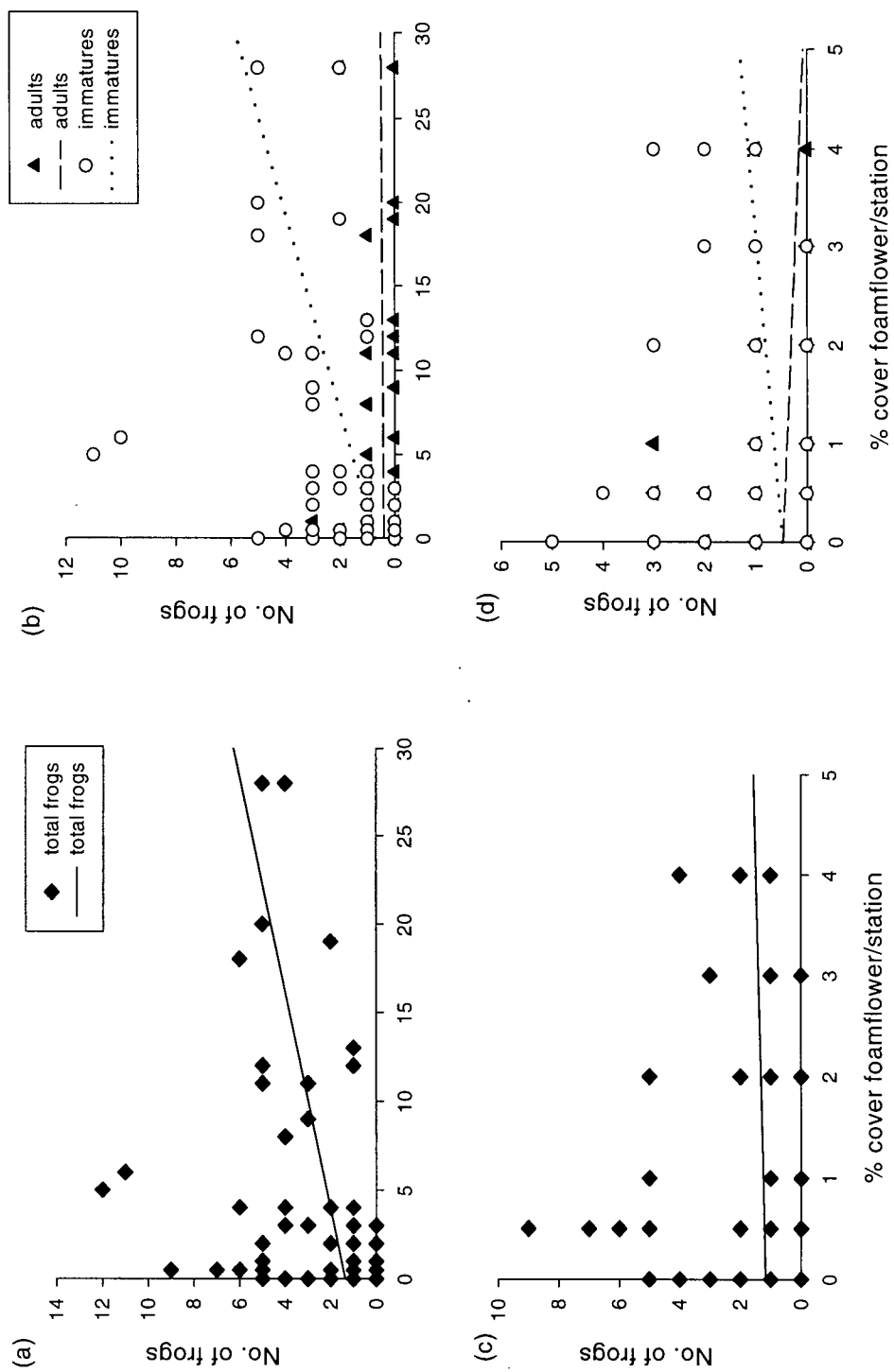


Figure 3.4. Frog numbers and corresponding regressions plotted for estimated percentage of foamflow cover at each pitfall station and (a) total frogs (all ages combined) and (b) adults and immatures. Due to the influence of the high number of Tamihi clear-cut captures, points were re-plotted excluding the Tamihi data for (c) total frogs (all ages) and (d) adults and immatures.

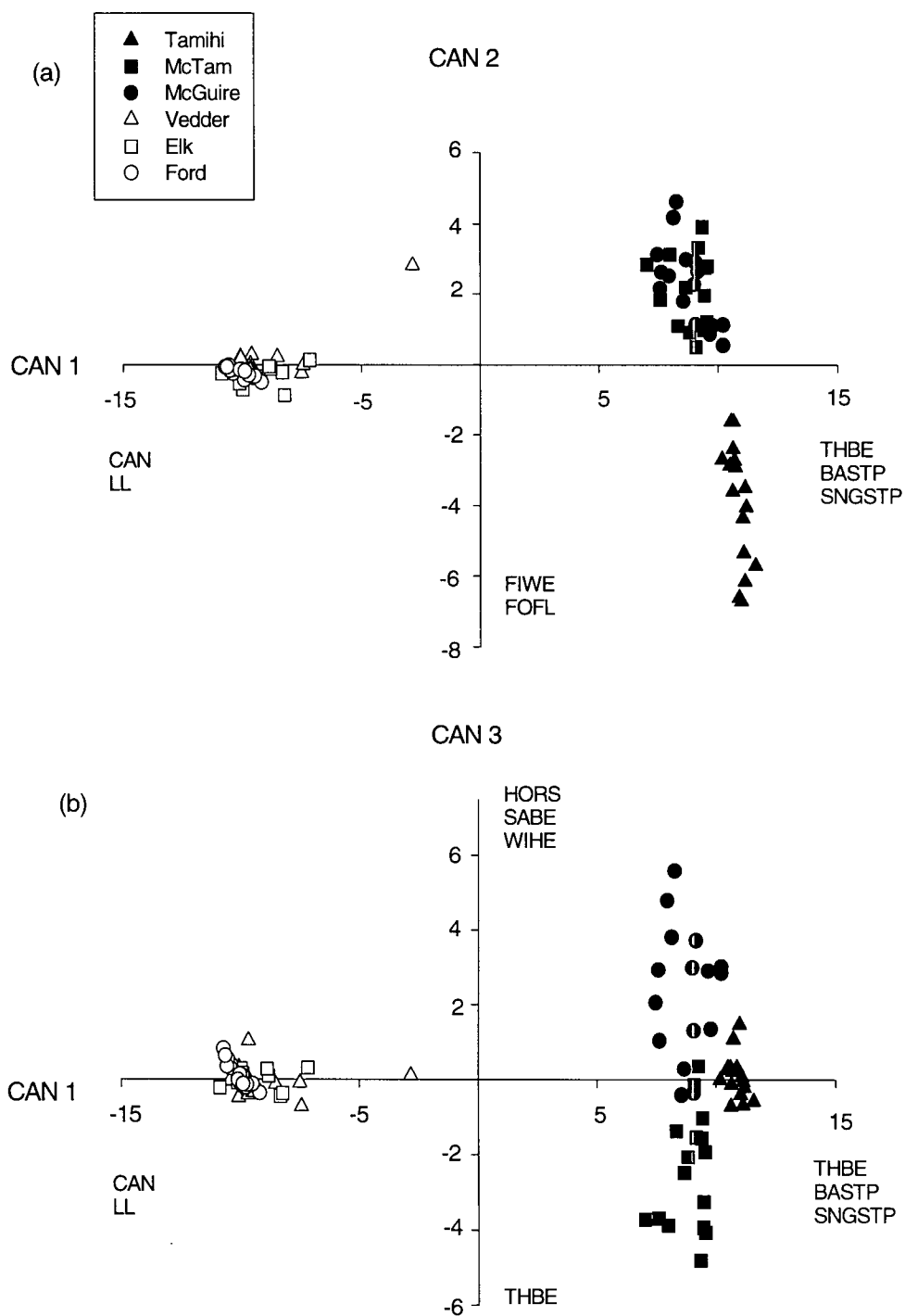


Fig. 3.5. Canonical analysis of the 16 habitat variables that most significantly grouped the six study sites. Tamihi, McTam and McGuire are clear-cut sites; Vedder, Elk and Ford are mature stands. The most relatively significant variables are indicated along the axes. (a) Habitat variables separated along Axis 1 (CAN 1) and Axis 2 (CAN 2), and (b) habitat variables separated along Axis 1 and Axis 3 (CAN 3).

Chapter 4. Conclusions, management implications and considerations for future research

The prediction that frog movement becomes restricted in clear-cut streams to within the riparian corridor was not supported, although it was apparent that age-specific responses did occur. Similarly, abundances also varied among age classes between the two habitat types. While significant site variation occurred, immature frogs were the main dispersers in both habitat types.

Although inferences about tailed frog populations based on these findings may be extrapolated to populations throughout the Pacific Northwest (e.g., WA, OR) where habitat characteristics (i.e., geography, geological formation, stand structure, soil composition, moisture regimes) are consistent with the variables assessed in this study, such generalisations should be made with caution. Timber removal may have variable effects on microclimate depending on local geography (Bury 1968), consequently resulting in variable responses to logging practices in environmentally distinct portions of the known range of *Ascaphus truei* (deMaynadier and Hunter 1995). This study demonstrated that significant variation occurs between sites within the same habitat type. Correct identification of “good quality” habitat is necessary to implement effective management plans for tailed frogs. The use of habitat characteristics to infer habitat quality is fraught with difficulties (Van Horne 1983). While not necessarily economically beneficial to timber licensees, long-term monitoring by combining pitfall traps and stream surveys may provide the best means of obtaining demographic information and distinguishing “source” and “sink” habitats for terrestrial stages of *Ascaphus*.

While it was difficult to isolate specific habitat requirements of tailed frogs that were not prone to spurious correlations, the differential age class responses by site suggests that applying blanket management practices to all areas with a similar habitat (i.e., managing for tailed frogs in the same way in all clear-cuts) may not serve in the best interests of species persistence. However, it is not economically feasible to conduct intensive surveys of all areas proposed for timber harvest, so a balance must be struck between the priorities of economics versus conservation. Rapid means of thoroughly assessing habitat quality for tailed frogs, particularly for limiting life stages, must be developed if the management goal is to achieve this balance. Ideally, this would be carried out during pre-harvest surveys, perhaps initiated on a coarse scale using maps and aerial surveys followed by ground-truthing for habitat suitability. In this manner, sites providing high quality habitat can be mitigated such that potential impacts on the existing population can be minimised or shifted elsewhere. Conversely, if habitat is deemed to be poor quality, then harvesting procedures need not be as rigorous towards maintaining already depauperate populations if populations in high quality areas nearby are maintained. However, in landscapes where populations are consistently low, then rigorous management may be required to prevent local extinctions.

Sampling terrestrial and aquatic habitats pre- and post-treatment is strongly recommended as it provides a more reliable means of immediately assessing proximate population responses to disturbance (Maxcy and Richardson 2000). It may also reveal local variation between sites in the same area, and provides a foundation upon which to lay management decisions that may be individually designed for the area being harvested.

Thus, management strategies should ideally be individually tailored towards the amphibian species of concern (Bury *et al.* 1991a).

This study demonstrated that even within a single species, there might be differential responses of age classes that may ultimately affect long-term maintenance of a population. The two principle findings indicated that clear-cut harvesting did not have strong effects on tailed frog movements. However, abundances did vary by age class, with adults more likely to be found in less disturbed, forested stands, and immatures more abundant in clear-cuts. Such differences may have ramifications on population dynamics over time, particularly if populations become more sensitive to environmental stochasticity (Schaffer 1981). Monitoring for changes in population responses over time, particularly assessing survival and mortality rates of the different age classes and/or sexes, will provide much needed information on population demographics of terrestrial forms. It will also help determine which age class/life stage may be the regulating factor in tailed frog populations (Sutherland 2000).

Given the phenotypic plasticity of anurans, clear-cutting may not necessarily result in any significant population effects. If such is the case, then management need not be warranted or required as intensively as speculated. The constraints of this study could not assess such large scale population responses. Nonetheless, negative effects of logging may occur within the habitat even though it may not have been revealed in this study. If the number of survivors is insufficient to maintain a viable population size, then local populations will decline over time, and two years is insufficient to detect such a trend. Due to the long period of time required to reach sexual maturity, such effects may lead to local extinction if mortality rates are high amongst metamorphosed frogs

immediately following clear-cutting. Conversely, the enhanced effect of site productivity after clear-cutting may mask time lags that occur in response to habitat alteration (Wiens *et al.* 1986; Stebbins and Cohen 1995).

As tailed frogs may live up to 15-20 years (Daugherty and Sheldon 1982a), it is reasonable to conduct studies of at least this duration, to assess long-term population dynamics. Effects on such long-lived species may not become noticeable until several years after a disturbance. If the effect is such that the population cannot recover, then *post-hoc* conservation measures will only offer a band-aid solution to a case where decline is imminent and no longer preventable. Marking individuals to record patterns of philopatry and survival is essential for experiments involving long-lived organisms. When the technology becomes accessible, it is recommended that that radio-telemetry be used to determine individual movements of tailed frogs.

Until such information is known, it may be best to provide habitat or "reserves" suitable to all life stages. One approach may be to enhance clear-cut habitat to make it more conducive to adult survival. However, this may be difficult to achieve given that the strongest correlations with adults were canopy cover and leaf litter, two factors that require the presence of trees. Selective harvesting methods that retain trees may offer some potential, although it is difficult to assess whether the effects would be strong enough to mitigate continued adult use of such areas if there is alternative habitat nearby that may be more conducive to survival and/or reproduction. Thus, providing forested areas adjacent to logged areas may allow adults to move into habitat more conducive to survival when an area is logged. Further studies are needed however, to determine the optimum size and shape of such tracts, and how movement may be affected by these

factors. Consideration must also be given to management priorities due to the implications of managing for a single species versus habitat or ecosystems, and the possible effects on other species occurring in the same management area.

As more frogs were found in forested stands closer to streamside, it may be best to retain characteristics of forests alongside streams, lending support to the call for the establishment of buffer zones in tailed frog streams (Bull and Carter 1996; Dupuis and Steventon 1999). Buffer strips should provide habitat to individuals. While there is little evidence (e.g., Bull and Carter 1996) indicating that the current 50 m buffer zones for tailed frogs in designated Wildlife Habitat Areas (Ministry of Forests 1999) is appropriate for terrestrial forms, buffers serve as movement corridors for amphibians (Rudolph and Dickson 1990; deMaynadier and Hunter 1995; Rosenberg *et al.* 1998; Lemckert and Brassil 2000), and may provide suitable habitat for frogs to disperse or seek refuge. It may also enhance the movement of tailed frogs parallel to streamsides relative to the perpendicular movement observed in this study. Buffers may also provide refuge for individuals ensuring the likelihood of recolonisation of depleted areas (Welsh 1990), while protecting the habitat integrity of a stream during and after timber harvesting. Future studies need to assess the effectiveness of buffers for all life stages of tailed frogs and other riparian dependent species in the area.

The presence of small, permanent streams or headwaters may be an indicator of tailed frog presence (Bury *et al.* 1991a) and rapid, preliminary surveys of streams within areas proposed for harvesting can confirm their presence. If high densities are revealed in these preliminary surveys (e.g., the Elk mature site), particularly adults, then more rigorous surveys can follow to determine the extent of habitat use within and beyond the

riparian zone. At this point, if there is a relatively long lead time before initiation of harvest activities in the area, then consideration may be given to the installation of pitfall stations and drift fences at various distances from streamside to assess activities of not only tailed frogs in the area, but other amphibians and small mammals. Conversely, if preliminary stream surveys reveal low densities of tailed frogs (e.g., Ford), then management procedures designed specifically for tailed frogs in the area need not be as intensive. However, the area must still be thoroughly assessed and managed for other wildlife species and values dependent on local habitat features and the regulations set forth by the FPC. It is also important that surveys and pitfall sampling be conducted at times of the year appropriate to tailed frog activities, rather than just provide an instantaneous "snapshot" in time that may reflect temporary conditions. Coverage over seasonal changes and preferably over the course of more than one year will help provide a more robust indication of population shifts.

In most cases, timber harvest plans are proposed far enough in advance to take into account these procedures. While it may add more time onto the planning phases, it economically benefits the timber licensee down the road when it comes time to actually extract the timber as management actions can be more efficiently applied depending on habitat essential to tailed frogs or sensitive species in the area. Thus it is important that efficient methods are developed to identify key habitat for such animals.

It is economically unrealistic to protect all habitats suitable for tailed frog populations, especially when other species and their needs must also be met. This can be accomplished by identifying habitats that have the greatest potential to provide refuge for source populations along with those with populations likely to persist over the long term.

Only then will management practices be effective in achieving the balance between meeting the needs of BC's forest industry while ensuring the sustainability of its flora and fauna.

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Appendix 1. Site histories for study grids in clear-cuts (Tamihi, McTam, McGuire) and mature stands (Ford, Elk, Vedder). For other site details, see Table 1, Chapter 2.

Tamihi

- Harvested 1993/94 using high-lead yarding
- Age at (first) time of harvest was 101-120 year old Western Hemlock/Red Cedar/Douglas Fir
- Replanted fall 1994/fall 1995 with Douglas Fir/Western Hemlock
- Aspect: south-facing
- Installation of pitfall traps April/May 1998
- Aerially sprayed (helicopter) with Vision® (glyphosate) September 1998 (single application; first time sprayed); 10-m no-spray buffer along streamsides
- Timber licensee: Tamihi Logging

McTam and McGuire

- Harvested 1995 for alder, maple and cottonwood; hand-felled, then yarded with 60' tower with chokers; ground-skidded over shallower areas
- Originally harvested 60-70 years ago for Red Cedar, Douglas Fir and some Grand Fir; grew back to hardwoods
- Replanted 1996 with Douglas Fir/Red Cedar
- Aspect: both north-facing
- McTam: installed pitfall traps August 1997; site repaired/re-opened May 1998
- McGuire: installed pitfall traps May/June 1998
- Aerially sprayed (helicopter) with Vision® (glyphosate) September 1998 (single application; first time sprayed); 10-m no-spray buffer along streamsides
- Timber licensee: Coast Mountain Hardwoods

Ford

- Ministry of Forests age class category 8 (141-250 years)
- Dominant vegetation: Douglas Fir
- Aspect: south-facing
- Installation of pitfall traps July 1997; site repaired and re-opened May 1998

Elk

- Ministry of Forests age class category 5 (81-100 years)
- Dominant vegetation: Douglas Fir
- Aspect: south-facing
- Installation of pitfall traps June 1998

Vedder

- Ministry of Forests age class category 5 (81-100 years)
- Dominant vegetation: Western Red Cedar/Broadleaf Maple (Minor: Red Alder/Birch)
- Aspect: south-facing
- Installation of pitfall traps June 1998

Appendix 2. Number of other amphibian species captured in pitfall traps in each site throughout the study period. Numbers reflect total captures only and do not account for age class or gender. Transect captures and larval frog and salamander captures from creek surveys are not included.

Count of Species	Mature Sites				Clear-cut Sites			
	Elk	Ford	Vedder	Total	McGuire	McTam	Tamhi	Total
Tailed Frog <i>Ascaphus truei</i>	51	13	24	88	4	6	77	87
Western Toad <i>Bufo boreas</i>	150			150	2	20		22
Red-legged Frog <i>Rana aurora</i>	2			2	2			2
Pacific Treefrog <i>Hyla regilla</i>		2		2				0
Pacific Giant Salamander <i>Dicamptodon tenebrosus</i>	19	1	4	24				0
Northwestern Salamander <i>Ambystoma gracile</i>	1			1	42	17		59
Long-toed Salamander <i>Ambystoma macrodactylum</i>	2		7	9	27	5		32
Ensatina <i>Ensatina eschscholtzi</i>	2	51	35	88	2	1		3
Western Red-backed Salamander <i>Plethodon vehiculum</i>	8	18	115	141		1		1
Roughskin Newt <i>Taricha granulosa</i>	1			1				0
Site Total	236	85	185	506	79	50	77	206

Appendix 3. Mean percentage, volume and area of variables per site that were measured at each pitfall station. Means are derived over all 16 stations in each site. Plant species and the nine other variables were visual estimates of relative percentage of area covered within the sampling plot used at the station. The top 15 most abundant plant species used in the habitat analysis (see Chapter 3) are listed first, followed by the remaining 75 species detected in the sites (arranged alphabetically by common name). " - " indicates that the species or variable was not detected in the site. Units for volume are in m³/ha and units for area are in m²/ha.

No.	Plant Species	Tamihi	McTam	McGuire	Vedder	Elk	Ford
1	elderberry, red <i>Sambucus racemosa</i>	1.14	5.10	3.27	2.79	1.13	-
2	fern, lady <i>Athyrium filix-femina</i>	4.07	4.88	6.72	1.69	4.55	1.00
3	fern, spiny wood <i>Dryopteris expansa</i>	1.71	1.42	0.91	1.25	0.50	2.25
4	fern, sword <i>Polystichum munitum</i>	1.64	3.00	3.70	12.63	4.75	6.58
5	fir, Douglas seedling <i>Pseudotsuga menziesii</i>	3.19	0.59	2.27	-	0.50	-
6	fireweed <i>Epilobium angustifolium</i>	23.31	0.93	2.36	-	-	-
7	foamflower <i>Tiarella trifoliata</i>	12.94	1.46	1.17	0.50	1.59	1.10
8	horsetail <i>Equisetum</i> sp.	-	0.50	7.37	-	0.50	-
9	Oregon grape, dull <i>Mahonia nervosa</i>	-	-	1.25	0.50	1.08	4.50
10	piggy-back plant <i>Tolmiea menziesii</i>	0.75	1.25	5.93	0.50	0.50	-
11	salmonberry <i>Rubus spectabilis</i>	3.77	2.43	10.31	7.14	3.00	-
12	thimbleberry <i>Rubus parviflorus</i>	8.31	14.81	11.31	0.50	0.50	0.50
13	thistle <i>Cirsium</i> sp.	0.58	2.73	2.06	-	-	-
14	vine maple <i>Acer circinatum</i>	-	-	2.25	22.29	-	22.91
15	willowherb <i>Epilobium</i> sp.	0.68	3.34	1.37	-	0.50	-
16	alder seedling <i>Alnus</i> sp.	-	-	3.11	-	0.50	-
17	Asteraceae	-	-	-	-	-	0.50
18	avens, large-leaved <i>Geum macrophyllum</i>	-	-	0.58	-	-	-
19	baneberry <i>Actaea rubra</i>	-	0.50	0.50	0.50	0.50	-
20	bedstraw, sweet-scented <i>Galium triflorum</i>	0.50	1.00	0.66	0.50	0.50	0.50
21	birch seedling, scrub <i>Betula glandulosa</i>	-	1.00	0.50	0.50	-	-
22	blackberry, trailing <i>Rubus ursinus</i>	-	-	-	-	-	0.89
23	bleeding heart, Pacific <i>Dicentra formosa</i>	0.50	0.64	0.75	0.50	-	0.60
24	bramble, five-leaved <i>Rubus pedatus</i>	3.73	-	-	-	-	-
25	brooklime, American <i>Veronica americana</i>	-	-	1.75	-	-	-
26	bunchberry <i>Cornus canadensis</i>	3.08	-	-	-	-	-
27	cascara <i>Rhamnus purshiana</i>	-	-	0.50	-	-	-
28	cedar seedling, western red <i>Thuja plicata</i>	-	0.50	4.33	0.50	0.60	2.50
29	coltsfoot, palmate <i>Petasites palmatus</i>	1.00	-	0.50	-	-	-
30	cottonwood, black <i>Populus balsamifera</i>	-	2.08	6.08	-	-	-
31	currant, red flowering <i>Ribes sanguineum</i>	0.50	0.50	0.50	-	-	-
32	dandelion <i>Toraxacum</i> sp.	-	0.75	0.50	-	-	-
33	devil's club <i>Oplopanax horridus</i>	0.50	1.00	1.20	7.00	1.00	-
34	dogwood, red-osier <i>Cornus sericea</i>	-	-	-	3.00	-	-
35	enchanter's nightshade <i>Circaea alpina</i>	0.50	1.29	1.53	0.77	0.69	0.50
36	false azalea <i>Menziesia ferruginea</i>	-	-	-	-	-	0.50
37	false Solomon's seal, star-flowered <i>Smilacina stellata</i>	-	-	-	1.13	-	0.50
38	falsebox/boxwood <i>Pachistima myrsinites</i>	-	-	-	-	-	0.50
39	fern, bracken <i>Pteridium aquilinum</i>	4.50	-	-	-	0.50	1.05
40	fern, deer <i>Blechnum spicant</i>	0.67	0.50	-	-	-	-
41	fern, licorice <i>Polypodium glycyrrhiza</i>	-	-	0.50	0.50	0.50	-
42	fern, maidenhair <i>Adiantum pedatum</i>	-	-	1.00	-	-	-
43	fern, oak <i>Gymnocarpium dryopteris</i>	1.00	0.68	0.50	0.50	0.50	-
44	fir <i>Abies</i> sp.	0.50	-	-	-	-	-
45	fir, amabilis seedling <i>Abies amabilis</i>	-	-	-	-	-	3.00

Appendix 3. Continued

No.	Plant Variables continued	Tamihi	McTam	McGuire	Vedder	Elk	Ford
46	fir, grand seedling <i>Abies grandis</i>	-	-	-	0.50	-	-
47	goat's beard <i>Aruncus dioicus</i>	0.50	-	-	-	-	-
48	gooseberry, black <i>Ribes lacustre</i>	0.80	1.31	0.82	0.63	0.50	0.50
49	grass Poaceae	-	0.60	2.42	-	-	-
50	hawkweed <i>Hieracium albiflorum</i>	-	0.50	-	-	-	-
51	hazelnut, beaked <i>Corylus cornuta</i>	-	-	-	0.50	-	-
52	hemlock, western <i>Tsuga heterophylla</i>	0.86	-	0.50	-	0.63	6.38
53	Herb-Robert/Robert Geranium <i>Geranium robertianum</i>	-	-	1.00	0.80	-	-
54	Hooker's fairybells <i>Disporum hookeri</i>	0.50	-	-	0.50	0.50	0.50
55	huckleberry, black <i>Vaccinium membranaceum</i>	1.04	-	-	-	-	-
56	huckleberry, red <i>Vaccinium parviflorum</i>	0.50	-	0.50	-	0.50	1.56
57	lily sp.	-	-	-	-	0.50	-
58	maple, bigleaf <i>Acer macrophyllum</i>	-	-	-	0.50	-	0.50
59	miner's-lettuce <i>Claytonia</i> sp.	0.50	1.47	0.50	0.50	0.50	0.63
60	mitrewort, 5-stamened <i>Mitella pentandra</i>	-	-	-	-	0.50	-
61	oceanspray/creambush <i>Holodiscus discolor</i>	-	-	-	-	-	1.00
62	pearly everlasting <i>Anaphalis margaritacea</i>	1.14	0.69	0.66	-	-	-
63	<i>Populus</i> sp.	0.50	-	-	-	-	-
64	prince's-pine <i>Chimaphila umbellata</i>	-	-	-	-	0.50	0.50
65	Queen's cup <i>Clintonia uniflora</i>	-	0.50	-	-	0.50	-
66	raspberry, black <i>Rubus leucodermis</i>	0.73	1.04	1.73	-	-	-
67	rattlesnake-plantain <i>Goodyera oblongifolia</i>	-	-	0.50	-	0.50	0.50
68	rose <i>Rosa</i> sp.	-	-	0.50	-	0.50	0.71
69	rush, wood <i>Luzula</i> sp.	1.18	1.21	0.50	-	-	-
70	salal <i>Gaultheria shallon</i>	-	-	2.00	-	-	2.00
71	Saxifragaceae	-	2.17	0.50	0.50	-	-
72	sedge <i>Carex</i> sp.	0.63	1.06	0.89	-	0.50	-
73	snowberry, common <i>Symphoricarpos albus</i>	-	-	0.50	1.00	-	0.50
74	sow-thistle, prickly <i>Sonchus asper</i>	0.50	-	0.50	-	-	-
75	speedwell, thyme-leaved <i>Veronica serpyllifolia</i>	-	-	0.58	0.50	-	-
76	starflower, broad-leaved <i>Trientalis latifolia</i>	-	-	-	0.50	-	0.50
77	sweet cicely <i>Osmorhiza</i> sp.	-	-	-	-	-	0.50
78	Trillium <i>Trillium ovatum</i>	-	0.50	-	0.50	0.50	0.50
79	twinkflower <i>Linnaea borealis</i>	-	-	-	-	0.50	0.67
80	twisted stalk, clasping <i>Streptopus roseus</i>	-	0.50	-	-	0.50	-
81	unknown sp.	-	-	-	-	-	0.50
82	vanilla leaf <i>Achlys triphylla</i>	-	0.50	-	0.60	0.50	-
83	violet <i>Viola</i> sp.	-	0.50	0.50	-	0.50	0.50
84	violet, stream <i>Viola glabella</i>	-	-	-	-	0.50	-
85	violet, trailing yellow <i>Viola sempervirens</i>	-	-	0.50	-	0.50	0.50
86	wall lettuce <i>Lactuca muralis</i>	0.75	1.47	0.88	0.50	0.50	0.96
87	wild ginger <i>Asarum caudatum</i>	0.50	0.50	-	-	1.25	0.50
88	willow <i>Salix</i> sp.	0.50	-	1.75	-	-	-
89	wintergreen <i>Pyrola</i> sp.	-	-	-	-	-	0.50
90	wintergreen, white-veined <i>Pyrola picta</i>	-	-	-	-	0.50	-

Appendix 3. Continued

Other Variables		Tamihi	McTam	McGuire	Vedder	Elk	Ford
1	bryophytes	2.63	5.63	12.28	5.78	17.34	34.38
2	lichen	0.50	0.55	0.54	0.50	0.59	0.72
3	fungi	0.50	0.50	0.67	0.50	0.50	0.50
4	bare ground (including mud)	5.50	6.69	7.44	10.31	9.88	6.06
5	leaf litter	6.69	5.94	5.63	45.69	39.56	47.25
6	rock	1.44	1.66	0.61	0.63	2.00	2.19
7	standing water	-	-	1.25	0.50	1.00	-
8	running water	-	-	4.00	-	4.00	-
9	overhead canopy closure	-	-	-	94.44	97.25	100.00

Woody Debris Variables		Tamihi	McTam	McGuire	Vedder	Elk	Ford
1	downed woody debris volume (decay class 1)	191.72	254.51	103.90	85.43	156.70	36.70
2	downed woody debris volume (decay class 2)	29.76	66.06	41.15	115.66	395.53	36.06
3	downed woody debris volume (decay class 3)	3.65	0.64	0.77	80.71	157.62	44.78
4	downed woody debris volume (decay class 4)	-	0.20	0.38	0.38	57.39	26.53
5	downed woody debris volume (decay class 5)	-	19.47	-	-	4.02	1.80
6	downed woody debris volume (decay class 6)	-	-	-	-	68.20	-
7	downed woody debris volume (decay class 7)	-	-	-	10.60	8.88	2.60
8	total downed woody debris volume (all decay classes)	225.12	340.88	146.20	292.78	848.34	148.47
9	stump volume	103.77	95.24	159.42	82.61	22.70	6.66
10	total volume (total downed woody debris + stumps)	328.89	436.12	305.63	313.43	851.18	154.17
11	basal area: conifers	-	-	-	57.91	69.24	88.54
12	basal area: deciduous	-	-	-	31.69	0.95	1.54
13	basal area total live trees	-	-	-	89.60	70.19	90.08
14	basal area snags	-	-	-	7.66	14.69	5.13
15	basal area stumps	239.70	159.51	187.67	9.97	7.72	16.72
16	basal area total dead (snags + stumps)	239.70	159.51	187.67	17.63	22.41	21.85
17	total basal area (dead + live)	239.70	159.51	187.67	107.23	92.61	111.93