Review and Synthesis of Literature on Tailed Frogs (genus *Ascaphus*) with Special Reference to Managed Landscapes

edited by:
Marc P. Hayes and Timothy Quinn

WASHINGTON STATE DEPARTMENT OF
Natural Resources
PETER GOLDMARK - Commissioner of Public Lands

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Washington State Forest Practices Adaptive Management Program

The Washington State Forest Practices Board (FPB) has established an Adaptive Management Program (AMP) by rule in accordance with the Forests & Fish Report (FFR) and subsequent legislation. The purpose of this program is to:

> *Provide science-based recommendations and technical information to assist the FPB in determining if and when it is necessary or advisable to adjust rules and guidance for aquatic resources to achieve resource goals and objectives. The board may also use this program to adjust other rules and guidance.* (Forest Practices Rules, WAC 222-12-045(1)).

To help provide the information needed to support adaptive management, the FPB established and empowered the Cooperative Monitoring, Evaluation and Research (CMER) committee to conduct effectiveness and validation monitoring in accordance with WAC 222-12-045 and Board Manual Section 22.

Report Type and Disclaimer

This technical report contains scientific information from research and monitoring studies designed to evaluate the effectiveness of the forest practices rules in achieving Forest and Fish performance goals, resource objectives, and/or performance targets. The document was prepared for the Cooperative Monitoring, Evaluation and Research Committee (CMER) and was intended to inform the Forest and Fish Adaptive Management program. The project is part of the Type N Amphibian Response Program, and was conducted under the oversight of the Landscape and Wildlife Advisory Group (LWAG).

This document was reviewed by CMER and was assessed through the Adaptive Management Program's independent scientific peer review process. CMER has approved this document for distribution as an official CMER document. As a CMER document, CMER is in consensus on the scientific merit of the document. However, any conclusions, interpretations, or recommendations contained within this document are those of the authors and may not reflect the views of all CMER members.

The Forest Practices Board, CMER, and all the participants in the Adaptive Management Program hereby expressly disclaim all warranties of accuracy or fitness for any use of this report other than for the Adaptive Management Program. Reliance on the contents of this report by any persons or entities outside of the Adaptive Management Program established by WAC 222-12-045 is solely at the risk of the user.

Historical Background

The original version of this review was done mid-2001 under contract with Glenn D. Sutherland, Cortex Consultants Inc. (1218 Langley Street, Suite 2a, Victoria, British Columbia, Canada V8W 1W2), at a time when all tailed frogs comprised one species, *Ascaphus truei*, with a nomenclature dating from its first description 102 years previous (Stejneger 1899). Tanya R. Wahbe was lead author on that effort and Sutherland and Linda A. Dupuis were co-authors. As happens, timing did not favor CMER, and though the original review was approved, partitioning of tailed frogs into two species (Nielsen *et al.* 2001) during the document's review process ultimately led to its rejection during peer-reviewed submittal. CMER declined to provide funding for the substantial revision needed to reflect this species reorganization, so this project became an unfunded mandate that Marc Hayes took on to complete. In evolving from its original 35-page form, Hayes retained original ideas and used sectional authorship to maintain recognition for the original authors. Further, the emergence of climate change from a background consideration to an unquestionable emerging threat over the period of revision led Hayes to add a section specifically addressing climate change issues that may impact tailed frogs.

Proprietary Statement

This review was developed with public funding, including contracts IAA 01-011. As such, it is within the public use domain. However, the concept of this work originated with the Washington State Forest Practices Adaptive Management Program and the editors. As a public resource document, this review should be cited as:

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Acknowledgements can be found in the last text section, which is consistent with the formatting of Northwest Fauna, the proposed peer-reviewed publication outlet for this document.

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Cooperative Management, Evaluation, and Research Committee (CMER)
The Landscape and Wildlife Advisory Group (LWAG) and
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EXECUTIVE SUMMARY

Tailed frogs comprise the only two living species in the genus *Ascaphus*, a group of frogs endemic to the Pacific Northwest (PNW) of North America. As the sister group of all other living frog species, tailed frogs have a unique array of primitive features, including true ribs; alternate-leg swimming; no functional tongue; and no voice and no auditory apparatus. Most frogs lack ribs; exhibit synchronous-leg swimming (a frog kick); and have a functional tongue, a voice, and an auditory apparatus. Tailed frogs also possess a unique set of skin peptides (ascaphins) with both anti-bacterial and anti-fungal properties.

Besides these primitive features, tailed frogs exhibit a number of other life history traits that tie them to permanent intermediate-gradient streams with substrates of at least a moderate clast size in north-temperate forested landscapes. These traits include relatively low temperature requirements, internal fertilization, a highly adhesive egg jelly, a rheophilous larval stage requiring interstitial streambed refuges, and post-metamorphic life stages that sustain high levels of water loss and turnover, have reduced lungs, and are active at extremely low light levels, typically at night. Adult tailed frogs exhibit high site fidelity, and populations appear to persist in streams where the aforementioned habitat characteristics are maintained over time, conditions frequent in perennial headwaters. However, tailed frogs also occur outside of headwater areas, but the actual extent of that distribution is unknown in part because sampling approaches for small headwater streams become less effective as stream size increases, and in part because interactions with other species (especially potential predators) become more frequent in larger streams, both of which may limit detecting tailed frog life stages. Process domain changes that alter flows and substrates, and inter-species interactions may limit tailed frogs in larger streams but the limiting dynamics and how these vary geographically remain largely unstudied.

Tailed frogs are also demographically distinctive. They have relatively low fecundity (a moderate clutch size and typically reproduce every other year), a lengthy larval stage (often more than a year), and a lifespan that may exceed 15 years.

This distinctive combination of features limits tailed frogs to relatively wet forested landscapes such as those found in particular areas of montane and submontane habitats of the PNW. The non-contiguous nature of suitable habitat may explain the divergence of the genus into two species: the Coastal Tailed Frog (*Ascaphus truei*) found in the Coast Ranges and Cascade Mountains of the Pacific Coast, and the Rocky Mountain Tailed Frog (*A. montanus*) found in the interiorly located Rocky Mountain axis.

Tailed frogs are of conservation concern throughout much of their geographic ranges because large proportions of their ranges are managed for timber, and disturbance associated with forest practices may reduce tailed frog habitat quality. Timber harvest in headwater stream basins can increase stream water temperature and reduce habitat moisture (through loss of stream and terrestrial canopy cover), increase sedimentation that results in loss of interstitial instream habitat, and contribute wood debris that can bury stream reaches. Tailed frogs appear to be less common in recently harvested areas relative to non-harvested areas, a pattern that may reflect less favorable temperature and moisture conditions or reduced levels of instream interstitial habitat. However, most studies addressing tailed frogs have been retrospective, and have lacked sampling techniques that estimate animal detectabilities. Further, the few experimental studies addressing tailed frogs have lacked statistical power.

In summary, current forest practices may negatively affect tailed frogs, but empirical evidence for this conclusion is weak. To better elucidate the effect of forest practices on tailed frogs, seven issues need address: 1) strengthen inference through manipulative experiments and detectability estimation; 2) consider interactions (biological or otherwise) that might affect treatment and reference sites differently; 3) partition the relative influence of effects generally thought to be positive (increases in productivity due to canopy removal) from those thought to be negative (increases in sedimentation); 4) increase recognition that differences exist in life history between the two tailed frog species that are likely to limit cross-species translation of study results (current understanding of the true level of differences between the two species are limited); 5) carefully consider altitudinal or latitudinal gradients, which modulate tailed frog response to disturbance, for potential inclusion as covariates in landscape-level experiments; 6) carefully consider the contrast between effect sizes and treatment effects in pilot studies prior to committing resources to major field studies; and 7) given the variability in field experiments, consider simulated stream studies in test channels where treatment variables (sediment inputs, temperature and light) can be more tightly manipulated while coupling such experiments in a sensible way to field conditions and experiments. Attention to these areas will greatly improve confidence in study results and the strength of inference from those results.

Despite the fact that sedimentation from roads linked to harvest almost invariably exceeds those of harvest itself, attention has been almost entirely focused on the effects of harvest *per se* on tailed frogs and other stream-associated amphibians. The one study examining the effects of road building on stream-associated amphibians was done outside of a forestry practices context. Hence, the relationship of common forest practices other than harvest *per se* on stream-associated amphibians needs attention.

Climate change will no doubt influence tailed frogs, and much of that impact is expected to occur via habitat alteration. The change driver is global in scope, so both currently recognized tailed frog species are likely to be affected rangewide. Moreover, habitat changes arising from climate change are anticipated to dwarf the most severe habitat effects known to affect tailed frogs in both scope and scale. Based on climate change predictions for the Pacific Northwest, we anticipate that significant changes in hydrology and stream temperature will influence tailed frog habitats, especially in headwater streams. Understanding climate change effects on tailed frogs will require experimental designs that consider both the shifts in seasonal temperature patterns and changes in stream hydrology that alter the riparian and stream ecology of their habitats.

INTRODUCTION, BACKGROUND AND SYSTEMATICS

Marc Hayes, Linda Dupuis, Glenn Sutherland, and Tanya Wahbe

This section provides basic background history, describes how we came to understand tailed frog distribution, and characterizes the data that led to current tailed frog systematics and taxonomy.

The Early Years (1897-1924): Leonhard Stejneger (1899) first described *Ascaphus truei*, the name applied to all populations of tailed frogs until 2001, based on a frog that Cloudsley Rutter accidentally caught during sampling for salmonid fishes on 19 August 1897 at a small tributary of Humptulips Creek, Washington (Van Denburgh 1912; M. Jennings, *pers. comm*.).[1] Stejneger did not indicate the sex of the specimen upon which he based his description (United States National Museum [USNM] 25979), but it was likely a female based on the fact that despite its size (40 mm snout-vent length [SVL]), it showed no indication of either the prominent cloacal "tail" or secondary sexual features characteristic of *Ascaphus* males (Figure 1). In his description, Stejneger recognized the species as distinctive and assigned the new genus and species to the frog family Discoglossidae[2] based on the presence of true (articulating) ribs and the transverse process at the base of the urostyle.[3] However, he also realized that *A. truei* differed from all known discoglossids in having the internal nares (choanae) positioned entirely between the vomerine teeth rather than in front of them. Further, Stejneger's limited dissection (based on the only specimen available) and partial destruction of its sternum (which occurred accidentally when Rutter had opened the body cavity for preservation in the field) limited his ability to identify the presence or absence of other important features. These included lack of an obvious auditory apparatus (tympanum and Eustachian tubes) and diverging lateral styles on the sternum, a feature that later investigators would associate with reduced lungs. The name Stejneger assigned to the genus derives from the latinized "A-" meaning without and "-scaphus" from the Greek *skapheion* meaning spade, referring to its lacking spadelike metatarsal tubercles, a feature linked with digging in many anurans. The species epithet honors Frederick True, then head curator of the Department of Biology at the United States National Museum.

During the first 50 years after its discovery, the focus on tailed frog study was on better characterizing distribution and improving morphological information to clarify its phylogenetic relationships. Edwin Cooper Van Dyke, who obtained one male *A. truei* from Paradise Valley in the vicinity of Reflection Lake[4] on Mount Rainier between 15-31 July 1905 (Van Denburgh 1912), made the second collection and the first outside of the Olympic Peninsula. This animal was lost in the San Francisco earthquake and fire of 1906, but John Van Denburgh (1912), who had examined it, discussed it along with three other adult males that Joseph Slevin had collected from Indian Henry's Hunting Grounds on Mount Rainier on 16-17 August 1911 (California Academy of Sciences [CAS] 30393-30395). Van Denburgh's contribution was his detailed description of the adult male, which verified the features Stejneger had left ambiguous; amplified the description of the

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[1] Van Denburgh (1912) gives the elevation of this locality as about 80 meters (265 feet).

[2] At the time of the description of *Ascaphus*, the Discoglossidae comprised exclusively Old World species.

[3] The distinctive elongate bone attached to the pelvic girdle of anurans thought to be the evolutionary derivative of caudal vertebrate (i.e., it represents fused caudal vertebrate).

[4] Van Denburgh (1912) gives the elevation of this locality as about 1,482 meters (4,861 feet).

skeleton; characterized the cloacal "tail" of males as the salient morphological feature for the genus (FIGURE 1), and first suggested it might be a sex organ; and mentioned the large (nuptial) pads on the inner surface of male carpi (thumbs). Joseph Slevin had also collected nine *A. truei* larvae (tadpoles) from near Lake Quinault, Washington over 1-6 August 1911 (CAS 29980-29988), but these tadpoles were not recognized as belonging to *A. truei* until well after Helen Gaige (1920) described the tadpole. Five years after the work of Van Denburgh, Joseph Grinnell and Charles Camp (1917) reported the first record of the species outside Washington State; a single frog collected 26 September 1909,[5] from the northwest slope of Craggy Peak in the Siskiyou Mountains of California. In the same year, Camp (1917) also reported the first record of the species in Oregon, a juvenile that Asa Chandler (Oregon State Agricultural School[6]) had collected along Red Creek 5 July 1915,[7] a secondary tributary of the of North Santiam River.

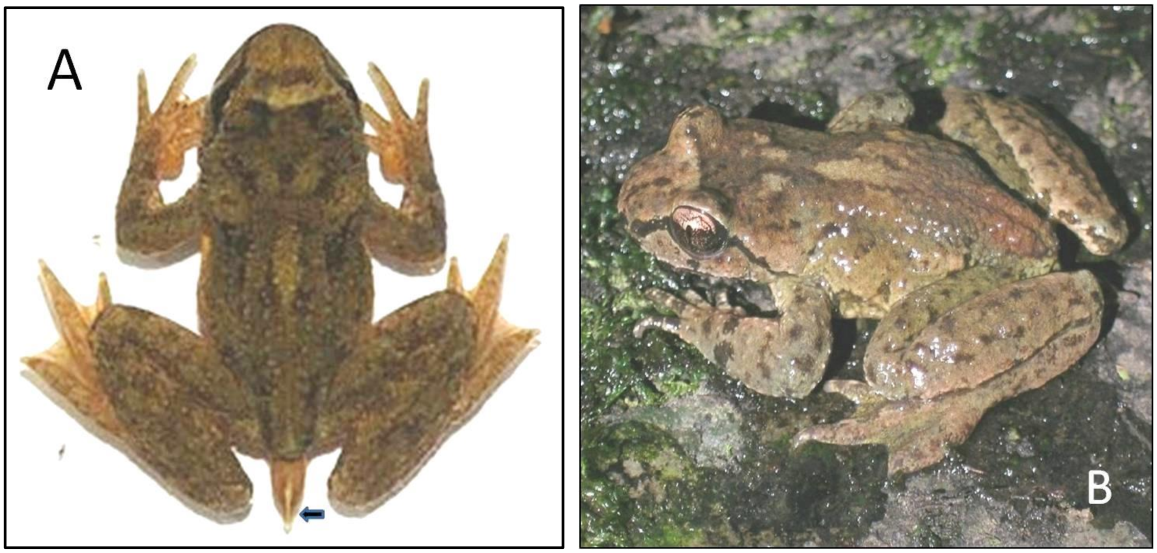

FIGURE 1. Male and female *Ascaphus truei*.

A. Male showing the cloacal tail (black arrow), the copulatory appendage that is their namesake. (Photograph credit: Wikipedia 2014) B. Female lacking the cloacal tail. Note the vertical pupil. (Photograph credit: Jennifer Dhundale)

Gaige (1920) provided the first information on the species based on a substantial number (>100) of animals, which she collected on the east side of the Olympic Peninsula between the slopes of Mount Steel (Jefferson County) to the north and McTaggart Creek (Mason County) to the south during the summer of 1919. This information included basic data on ecology and habitat use, detailed morphological descriptions with information on colors of the adults and tadpoles (FIGURE 2) from life, and the first descriptions of eggs and

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[5] This collection, which preceded the Slevin collections by two years, was not reported until Van Denburgh (1912) had drawn attention to the species.

[6] Oregon State Agricultural School ultimately became Oregon State University.

[7] Camp (1917) did not report the date of collection. The collection date and habitat information exists in a 1 November 1916 letter from Asa Chandler to Camp in which he states, “The specimen was obtained in Red Creek in the Santiam National Forest, Linn Co., Oregon, at an elevation of about 3000 ft., July 5, 1915. It was found at the edge of the creek mentioned – a bouldery mountain stream of very cold and very swift water in a heavily wooded spot – moss covered logs, etc. abundant. The location is in the Canadian zone – Douglas Fir, *Pinus montanus*, Hemlock, etc."

oviposition sites.[8] Gaige (1920) provided notable information on how to sample for *Ascaphus*, which involved turning "every moveable rock in the stream" to aid in their detection; the stream-associated nature of the habitat in which most post-metamorphic animals were found; the sexual dimorphism in size in favor of females; the prominent change in sexual characteristics of males during breeding, the temporal distribution of those male characteristics of which she took to indicate a prolonged breeding season; additional secondary sexual characteristics in males consisting of dark excrescences on the inner side of the first two fingers and a rounded area on the forearm; and the first observations suggesting that timber harvest might influence tailed frog ecology.

FIGURE 2. Two larvae (tadpoles) and a metamorph (foreground) of *Ascaphus truei*.

Note the white spot on the end of the tail of the larva in the background. (Photograph credit: Ryan O'Donnell)

Katherine Van Winkle (1922) extended knowledge of *A. truei* distribution along the west slope of the Washington Cascades north to close to North Bend. She repeated Van Denburgh's (1912) suggestion that the "tail" of males was a copulatory organ based on the ventral location of the cloaca (vent) near its tip, and noted that the base of the "tail" and adjacent femoral region were distinctly papillose. Van Winkle was also the first to

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[8] Tailed frog oviposition sites have sometimes been termed nests (e.g., Adams 1993, Bury et al. 2001), but no evidence currently exists that females alter the near-space environment around deposited eggs, the condition required for an oviposition site to be labeled a nest.

record *A. truei* some distance from water under wet conditions; and she described another secondary sexual characteristic for breeding males: the dark excrescences on each side of the pectoral region of the chest**.**

The Noble Revolution (1925-1948): Combining field and laboratory observations with experiments, Kingsley Noble (1925, 1931; Noble and Putnam 1931) ushered in a new era of understanding and insight into *Ascaphus* biology. His identification of large masses of spermatozoa in the lumen of female *Ascaphus* oviducts and notably in glands of the posterior oviducts indicated that fertilization was internal (Noble 1925). Noble was also first to identify the keratinized spines concealed within the cloaca of the non-breeding male that become visible during breeding as blood filling the “tail” makes it turgid and cloacal eversion exposes the spines. Noble’s (1925) observations that breeding males readily extend their cloacal "tails" forward led him to suggest that this organ is pressed against the cloaca of the female in copulation, a supposition he and others (Noble and Putnam 1931, Slater 1931, Wernz 1969) later confirmed. Noble was also the first to thoroughly explore the relationship of *Ascaphus* among amphibians. In particular, he pointed out its lack of a voice; general copulatory mechanism; vertebral structure; muscles of the chest, upper arm, and thigh; and venation of the posterior trunk was more similar to that of salamanders than all other anurans (Noble 1925, 1931),[9] which set the stage for subsequent suggestions that *Ascaphus* was the sister group of all extant anurans. Furthermore, investigators up to Noble had simply continued to accept its classification, originating with Stejneger (1899), as a discoglossid (e.g., Van Denburgh 1912, Gaige 1920). The distinctive suite of features that Noble (1931) identified in *Ascaphus* led him to erect a separate family, the Liopelmatidae,[10] for both *Ascaphus* and the unique New Zealand frog genus *Leiopelma*, based on characters they seemed to share. This familial-level arrangement became the accepted classification over the next nearly 50 years.

Over the 17 years after Noble’s seminal compendium (1931), work addressing *Ascaphus* reverted almost entirely to refining knowledge of its distribution. George Myers (1931, 1943) provided the second record from California, extending its known range south into Humboldt County, and provided limited data on the ecology of its tadpole. Following Myers, Hobart Smith (1932) provided the first record from Montana and the Rocky Mountains based on one larva collected 9 August 1931 a few kilometers east of St. Regis Pass; this record is the first subsequently attributable to *A. montanus*. Based on two adults collected in August 1931, Arthur Svihla (1933) extended the known range of *Ascaphus* in Washington north to Whatcom County. Svihla also provided the first report of *Ascaphus* on the east side of the Cascade Mountains in Washington based on a series collected at Thetis and Box Canyon Creeks in the upper Yakima River drainage on 4 September 1931 (Svihla and Svihla 1933). In the same year, Jean Linsdale (1933) provided the first records for *Ascaphus* in Idaho based on 10 animals collected in the vicinity of Black Lake and Cuddy Mountain from 10 June 1930-1 July 1932; these records are also the first post-metamorphic specimens attributable to *A. montanus*. In August-September 1933, Lauren Donaldson (1934) reported the first occurrence of *Ascaphus* east of the continental divide based on five larvae collected at Midvale Creek below Glacier National Park (Montana).

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[9] Salamanders are the most generalized of modern (extant) amphibians groups in that they exhibit the suite of features most likely to have existed in the ancestor to all amphibians.

[10] When Noble (1931) erected the family name, the spelling was Liopelmatidae; the currently accepted spelling of the same family name is Leiopelmatidae.

In 1935, William Ricker and Shelley Logier (1935) reported the first records from Canada based on collections from several streams around Cultus Lake, British Columbia (6 km [3.7 mi] north of the US border) made between 9 June and 15 September 1934. Based on two adult males collected 21 May 1934 and a larva and an adult male observed May 1935, all from 18 km (11.2 mi) above the mouth of the Rogue River, Henry Fitch (1936) reported the second records for Oregon. Based on one larva collected on 25 June 1934 during a Bureau of Fisheries stream survey on French Creek (Siskiyou County), Leo Shapovalov (1937) reported the third *Ascaphus* record for California.

The 1940s saw reports continue to extend the known range of *Ascaphus* north and east into British Columbia, and further south in Montana. Based on two juveniles collected on the steep eastern slope of the Fraser Valley about 24 km (14.9 mi) south of Lytton on 20 June 1941, John Slipp and Clifford Carl (1943) extended the known range 169 km (105.0 mi) north and east of the Ricker and Logier (1935) Cultus Lake locality. Carl and Ian Cowan (1945; see also Carl 1949) then reported on an adult male collected 48 km (29.8 mi) north of Vancouver and 10 km (6.2 mi) above the mouth of the Indian River on 5 November 1942. Based on one individual collected on 22 July 1932 at Camas Lake (Ravalli County), Montana, Thomas Rodgers and William Jellison (1942) extended the known range 272 km (169.6 mi) south of the Midvale Creek locality reported by Donaldson (1934).

Early Systematic Efforts (1949-1978): Myron Mittleman and George Myers (1949) were the first to characterize variation across the geographic range of tailed frogs. Based on morphology, they recognized three allopatric subspecies: *A. t. californicus* for frogs from Del Norte, Humboldt and Siskiyou Counties in northwestern California, *A. t. montanus* for frogs from the Rocky Mountains,[11] and *A. t. truei* for frogs from the Cascade and coastal mountain axes of Oregon and Washington.[12] Mittleman and Myers (1949) distinguished *A. t. californicus* from the remaining two subspecies based on its relatively larger eyes (eye-to-body size ratio ≥13.6 percent versus ≤13.5 percent in the remaining two subspecies) and reduced number of vomerine teeth (≤7 versus ≥8 in the remaining two subspecies). The subspecies *A. t. montanus* was distinguished from *A. t. truei* by the latter's relatively small eyes (eye-to-body size ratio ≤11.9 percent versus 12.3-13.5 percent in *A. t. montanus*) and its relatively narrower head (head width-to-body size ratio ≤35.2 percent versus 35.6-38.6 percent in *A. t. montanus*). Robert Stebbins (1951) recognized the utility of understanding morphological variation, but resisted using these subspecific labels. Thus, later workers rarely used Mittleman-Myers (1949) trinomials.

The next two decades witnessed further refinements in the understanding of *Ascaphus* distribution in British Columbia, California, Idaho, and Washington. George Salt (1952) extended the known range of *Ascaphus* over 110 km [68.4 mi] to the south of Myers' (1931) record when he obtained a juvenile from a small stream in Russian Gulch State Park, coastal Mendocino County, California on 20 June 1951. Carl (1955) extended the known range of *Ascaphus* over 190 km (118.1 mi) to the north of the previous northernmost point he and Cowan had reported in 1945 based on an adult male found 12

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[11] Mittleman and Myers (1949) did not examine material from eastern Washington and eastern Oregon (i.e., the Blue and Wallowa Mountains) because the first collections from these areas were made after they finished their work.

[12] Though *Ascaphus* was known from British Columbia (Ricker and Logier 1935, Slipp and Cowan 1943, Carl 1945), it was known from few sites, making little material available for study and was not included in the Mittleman and Myers (1949) analysis.

September 1954 in a damp creek bottom at Hovel Bay, British Columbia. In a compendium summarizing the distribution of amphibians in Washington State, James Slater (1955) assembled specimen-verifiable records of *Ascaphus* for Washington State. This summary recorded *Ascaphus* from every county on the Olympic Peninsula; all counties on the west slope of the Cascade Mountains except for Clark and Cowlitz; and Chelan, Kittitas and Yakima Counties on the east Cascade slope. Notably, records from counties encompassing the Willapa Hills or Blue Mountains were absent. Carl Corbit (1960) extended the inland range of *Ascaphus* in Idaho to the north, south, and southeast of the records provided by Linsdale (1933). One year later, James Grant (1961) extended the inland range of *Ascaphus* over 100 km (62.1 mi) further north into British Columbia. Dean Metter (1964a) provided the first discussion of *Ascaphus* populations from the Blue Mountains of Washington. Moreover, his careful contrast of *Ascaphus* from the North Fork of the Touchet River in the Blue Mountains with those from the Palouse River headwaters in Idaho revealed more within-population variation than observed among the subspecies erected by Mittleman and Myers (1949), further reducing confidence in the utility of their subspecific labels. Metter (1964a) also provided the first substantial ecological information on tailed frogs from the Rocky Mountain axis, which revealed ecological differences when compared to Cascade axis populations. Assembling available records for *Ascaphus* in California, Bruce Bury (1968; see also Bury *et al.* 1969) showed that its distribution extended substantially inland (i.e., into Trinity, Shasta, and Tehama Counties) and that it occurred in areas with at least 102 cm (40 in) annual precipitation.

Metter and Robert Pauken (1969) used phenetic multivariate statistical distance[13] to characterize morphological variation among *Ascaphus* populations in Idaho, Oregon, and Washington; and computer mapping techniques to display their results (Pauken and Metter 1971). Their analyses revealed substantial morphological variation that was difficult to interpret. Among post-metamorphic individuals, close morphological similarity existed between populations only where geographic barriers were minimal. Larvae showed a high morphological similarity except where the characteristics of their natal streams were quite different, which was independent of geography, even at a regional scale. Metter and Pauken (1969) concluded that *Ascaphus* larvae seemed well adapted to their habitat and isolation related to geographic distance was unlikely to result in notable changes in larval morphology. Selection for features contributing to larval survival in fast-moving streams appeared to dominate larval morphology.

Modern Approaches Leading to Current Understanding (1979-Present): As a part of his dissertation, Charles Daugherty (1979) used allozymes[14] in renewed effort to characterize variation across the geographic range of tailed frogs. His analysis revealed genetic groups concordant with the two major geographic areas occupied by the genus: the Coastal Range-Cascade and Rocky Mountain axes. Daugherty did not formally recognize these differences through taxonomic revision (i.e., by naming new species), but his genetic data were ultimately incorporated into later systematic work (see Nielson *et al.* 2006).

Greater perspective on the relationships of *Ascaphus* emerged in the 1980s and 1990s. David Green, Daugherty, and James Bogart (1980) discovered that *Ascaphus* possesses a

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[13] Phenetics consists of those systematic approaches that classify organisms based on overall similarity, usually in morphology or other observable traits, regardless of their phylogeny or evolutionary relationships.

[14] Allozymes are proteins coded by particular genes that are used for genetic or phylogenetic analysis.

diploid chromosome number of 46, and even more distinctively, that it has the largest number of telocentric[15] chromosomes of any diploid anuran. The latter fact and substantial dissimilarity to the karyotype of its presumptive New Zealand relative, *Leiopelma*, led Green and colleagues to erect a new family exclusively for *Ascaphus*, the Ascaphidae. Moreover, subsequent genetic examination of *Leiopelma* using allozymes (Green *et al.* 1989) reinforced the idea that *Ascaphus* and *Leiopelma* were not closely related, and helped support the idea that *Ascaphus* is the sister group to all other anurans. Sperm cell studies (Jamieson *et al.* 1993, Lee and Kwon 1996, Kasinsky *et al.* 1999) and mitochrondial protein-coding gene studies (Gissi *et al.* 2006) have helped reinforce the latter. The finding of Bogart and colleagues (1994) that *Ascaphus*' karyotype was very similar to the 48-chromosome karyotype of the well-known lobed-fin fish, *Latimeria chalumae*, further reinforced the notion of its primitive ancestry. *Latimeria* had long been regarded as a living fossil reflecting a lineage similar to that which gave rise to tetrapods, including amphibians (Forey 1980, Gorr *et al.* 1991). Using mitochondrial ribosomal RNA genes, Jennifer Hay and her colleagues (1995) found that *Ascaphus* is included within the monophyletic[16] group that includes all anurans and provided data that would seem to contradict the idea that *Ascaphus* is the sister group of all other anurans. However, more recent data suggest that mitochondrial ribosomal RNA genes lack the temporal resolution to address the sister group question (Hertwig *et al.* 2008). Even the larvae of *Ascaphus*, which are a classic example of a tadpole with suctorial mouthparts,[17] show characteristics indicative of the historically ancient nature of the taxon (Haas and Richards 1998).

The 1980s onwards also saw additional refinements to the understanding of *Ascaphus* distribution in California, Idaho, Oregon, and Washington. Primarily as a consequence of electroshocking studies on sculpins, Owen Maughan and colleagues (1980) considerably refined the knowledge of *Ascaphus* distribution in central Idaho and the upper panhandle. They indicated that *Ascaphus* was widespread, but appeared spottily distributed in headwaters. In finding that *Ascaphus* was not detected in all headwater streams, Maughan and colleagues (1980) concluded that the spotty distribution might have resulted from previous climatic conditions associated with glacial advance and retreat, sampling bias or some unknown ecological factor linked to elevation. Further, based on a hypothesis that *Dicamptodon* would ultimately be found across a northerly boreal connection between the Cascade and Rocky Mountains (Maughan *et al.* 1976), Maughan and colleagues (1980) speculated that *Ascaphus* would be found to have a parallel boreal connection. Based on five individuals collected 3.2 km (2.0 mi) southeast of the confluence of Elder Creek and the south fork of the Eel River, Hart Welsh (1985) recorded the species 20 km (12.4 mi) inland from the southernmost locality in its geographic range in California. Based on individuals collected respectively, 2.6 km (1.6 mi) south of State Route 6 on a tributary of the Willapa River on 15 August 1992 and 21 km (13.0 mi) north of Cathlamet on a tributary of the Elochoman River on 29 April 1993, Michael Adams and Albert Wilson (1993), and Steven Manlow (1994) provided the first records for the

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[15] Telocentric chromosomes are those that have terminally joined chromosomal arms.

[16] An evolutionarily cohesive group in which all members of the group share the same recent common ancestor.

[17] Suctorial mouthparts are a morphology that appears to have evolved independently several times among "advanced" frogs (i.e., Neobatrachia) regardless of phylogenetic relationship. The Neobatrachia consists of a large monophyletic group consisting of over 90% of all extant frog species (over 30 different families of frogs) but excludes the 10 more primitive frog families (Frost et al. 2006).

Willapa Hills in southwest Washington State. Up to that time, the Willapa Hills had been largely unexplored because commerical timberlands comprised over 95 percent of the region, and access to much of its ownership had been historically limited. Based on an *Ascaphus* collected on Williams Creek 0.3 km (0.2 mi) southwest of the Twisp River in Okanogan County, Washington, Dana Visalli and William Leonard (1994) contributed to filling the 180-km (112-mi) distribution gap between Chelan County, Washington, and the east slope of the Cascade Mountains in British Columbia. Evelyn Bull and Bernie Carter (1996a) clarified the distribution of *Ascaphus* in the Blue Mountains of northeast Oregon. Based on several specimens and photographs of *Ascaphus* from Baker, Shotgun, and Little Shotgun Creeks (secondary tributaries of the Pit River) obtained on 30 March and 4 April 1994, Lee and Matthew Simons (1998) extended knowledge of the distribution of *Ascaphus* inland in California over 30 km (18.6 mi) east of Bury's Shasta region reports (1968; see also Bury *et al.* 1969). Similarly, in January-March 2002, Richard Nauman and Deanna Olson (2002) recorded two subadult *Ascaphus* along Beartrap Creek, a locality 23 km (14.3 mi) north of the Bury and colleagues (1969) reports.

Based on data from a composite of time- and area-constrained surveys at 733 sites during the interval 1995-1998, Linda Dupuis and colleagues (2000) developed a more thorough understanding of tailed frog distribution in British Columbia than previously available. In particular, they recorded tailed frogs as fairly continuous across coastal British Columbia from somewhat south of the Nass River. Dupuis and colleagues (2000) also found *Ascaphus* in a disjunct region in southeast British Columbia, where they recorded tailed frogs in 10 tributaries of Flathead River near the Montana (US) border and in six tributaries of the Yahk River (upper Columbia River). Their analysis seems to refute the boreal connection hypothesis of Maughan and colleagues (1980), though some of the intervening area still remains unexamined. Tailed frog distribution over coastal British Columbia generally corresponds to the Coastal Western Hemlock biogeoclimatic zone, whereas in southeast British Columbia, the species occurs within a small segment of the Engelmann Spruce (*Picea engelmannii*)/Subalpine Fir (*Abies lasiocarpa*) biogeoclimatic zone. In the same year, Kermit Ritland and colleagues (2000) conducted an RAPD[18] survey of 22 *Ascaphus* populations from four regions in British Columbia. They found that the interior populations (Flathead/Yahk complex) were the most distinct group, but they concluded that the genetic distance between interior populations and other regions was equal to that expected from isolation by physical distance alone (as opposed to phylogenetic differentiation) and hence, did not partition the species.

Marilyn Nielson and colleagues (2001) recommended that inland populations be recognized as a distinct species to accurately reflect their independent evolutionary history and the diversity within *Ascaphus* based on two lines of evidence: the divergence in mitochondrial haplotypes of cytochrome and dehydrogenase genes between coastal and inland populations of *Ascaphus* and divergence in allozyme and morphological data from these same populations. Coastal populations, labeled Coastal Tailed Frog, kept the

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[18] Random amplification of polymorphic DNA (RAPD) is a type of Polymerase Chain Reaction (PCR), but the segments of DNA that are amplified are random. Several short primers (8-12 nucleotides long) are used with PCR on a large template of genomic DNA with the resultant amplification of certain fragments. Semi-unique profiles can be resolved in little-studies biological systems, but its resolving power is much more limited than targeted, species-specific DNA comparison methods.

name *A. truei* as the type locality (near Humptulips, Washington) comprises part of this population system; the inland species, labeled Rocky Mountain Tailed Frog, was named *A. montanus*, based on the Mittleman and Myers (1949) subspecific name given to these populations. In this effort, Nielson and colleagues (2001) did not analyze populations from British Columbia and the analysis of Ritland and colleagues (2000) was not addressed in their work. However, the inland Flathead-Yahk complex that Ritland and colleagues (2000) found to be the most differentiated and that is disjunct based on the work of Dupuis and colleagues (2000), is believed to represent *A. montanus* (Adams and Pearl 2005b). The recent work of Michael Conlon and colleagues (2007) that addressed skin peptides revealed a dichotomy between populations allocated to *A. truei* versus *A. montanus*, which supports the species partitioning of Nielson and colleagues (2001).

Based on allozyme and mitochondrial DNA sampled over a greater range of populations, Nielson and colleagues (2006) provided a more detailed analysis of the variation within *Ascaphus*. This work not only supported the previous species partitioning, but indicated that evolutionarily significant units (ESUs) also exist within each species. In particular, populations within the Olympic Mountains (Washington) and the Siskiyou Mountains (California and Oregon) seemed to show significant differentiation within *A. truei*, and populations south of the South Fork of the Salmon River (Idaho) and north and west of the Salmon River (including the Blue Mountains [Oregon and Washington], the Wallowa Mountains [Oregon], and the Seven Devils Mountains [Idaho]) appeared to show significant differentiation within *A. montanus*. Unfortunately, this broader analysis also excluded populations from British Columbia, so notwithstanding the conclusion of Dupuis and colleagues (2000) that interior British Columbia populations are disjunct, their taxonomic status has remained slightly ambiguous as a result of the aforementioned conclusions of Ritland and colleagues (2000). Variable support for population clustering in both species of tailed frogs within unnamed ESUs, and among ESUs or other population clusters indicated by Nielson and colleagues (2006) requires corroboration; and taxonomic recognition of any units within either tailed frog species has not occurred.

Coastal Tailed Frog (*A. truei*) and Rocky Mountain Tailed Frog (*A. montanus*) represent the current nomenclature that recognizes the diversity within *Ascaphus* (Crother 2008). In addition, we assume in this review that the conclusion of Dupuis and colleagues (2000), that interior British Columbia populations of *Ascaphus* are disjunct, is indeed correct, and that on biogeographic grounds, they represent part of the *A. montanus* population system. Nonetheless, we emphasize that this hypothesis remains to be verified because tailed frog populations in Canada and the United States have to date never been combined into a single analysis.

In the rest of this review, we use the following conventions. Where data explicitly pertain to one of the two species of *Ascaphus*, the species to which those data are attributable is identified. Species attribution based on studies prior to the Nielson and colleagues' (2001) partitioning of the tailed frog species is done based on geographic information provided in those studies. Rarely, a single data set includes both species in a form that cannot be effectively partitioned; we caution that those data may need to be re-examined in a species-specific way. Additionally, we caution readers to also consider that phylogeny may contribute to differences among intraspecific populations at the ESU scale.

DISTRIBUTIONAL SUMMARY

Linda Dupuis, Marc Hayes, Glenn Sutherland, and Tanya Wahbe

Range of Tailed Frogs in North America: The range of tailed frogs in North America generally encompasses the more mesic and pluvial portions of the coastal and interior mountains of the PNW (FIGURE 1). Tailed frogs appear to be absent from more xeric and low-gradient habitats, which include alluvium-dominated lower elevation valleys (e.g., the interior basin of the Columbia River and its riverine tributaries) and the most rain-shadowed portions of interior ranges (Dupuis *et al.* 2000). Major political entities that encompass this known range include the Canadian province of British Columbia (Matsuda *et al.* 2006), and in the United States, California (Jennings and Hayes 1994), Idaho (Groves 1994), Montana (Werner *et al.* 2004), Oregon and Washington (Jones *et al.* 2005).

Ascaphus truei: The range of *A. truei* encompasses the coastal portions of the geographic range of tailed frogs in the states of California, Oregon, and Washington, and the province of British Columbia (Adams and Pearl 2005a; FIGURE 1). Most of the range of *A. truei* occurs west of the Cascade Mountains (Jones *et al.* 2005) and major coastal ranges in British Columbia (Dupuis *et al.* 2000). These mountains generally receive more precipitation on their windward than on their leeward sides; hence, the windward (west) sides generally display a more humid climate. Dupuis and colleagues (2000) discussed one exception to this general pattern from the extreme northern end of *A. truei* range. Near Prince Rupert, *A. truei* populations on the windward side of the mountains seem small and scattered as opposed to large and widespread on the leeward side. The windward side of these coastal mountains receives extremely high annual precipitation ($\bar{x}$ = 4400 mm) compared to their leeward side ($\bar{x}$ = 2300 mm), so Dupuis and colleagues (2000) suggested that high precipitation levels, which is linked to more frequent and intense rainfall, might expose *A. truei* aquatic life stages to more frequent and extreme stream bedload transport events that might limit windward populations.

The pattern of *A. truei* distribution lapping onto the east (leeward) side of the Cascade Mountains (and coast range mountains in British Columbia) varies considerably as an apparent gradient with latitude. In particular, *A. truei* has not been recorded on the east slope of the Cascade Mountains from the Klamath Basin southward in Oregon, though considerable effort has been devoted to detecting the species in this region (Hayes 1995, M. Hayes, *unpubl. data*). The species may be absent because mesic stream-edge habitats are rare in this region and no low-elevation (<1,400 m [4,600 ft]) trans-Cascade passes are available to facilitate a connection with westside populations and the eastward movement of maritime air. To the north, on the west side of the Deschutes Basin (Oregon), a few scattered records appear east of the Cascade Mountains. For example, Smith (1997) reported *A. truei* from Wilson Creek on the Warm Springs Reservation (45.0897°N, 121.6138°W); two relatively low passes, Blue Box (1,227 m [4,024 feet]) and Abbott (1,070 m [3,511 ft]), are nearby. In Washington, many records of *A. truei* exist on the east slope of the Cascade Mountains (Dvornich *et al.* 1997); and in British Columbia, a number of records also occur on the east slope of coast range mountains (Dupuis *et al.* 2000). However, as noted by Dupuis and colleagues (2000), except for the Prince Rupert example, tailed frogs become increasingly infrequent with

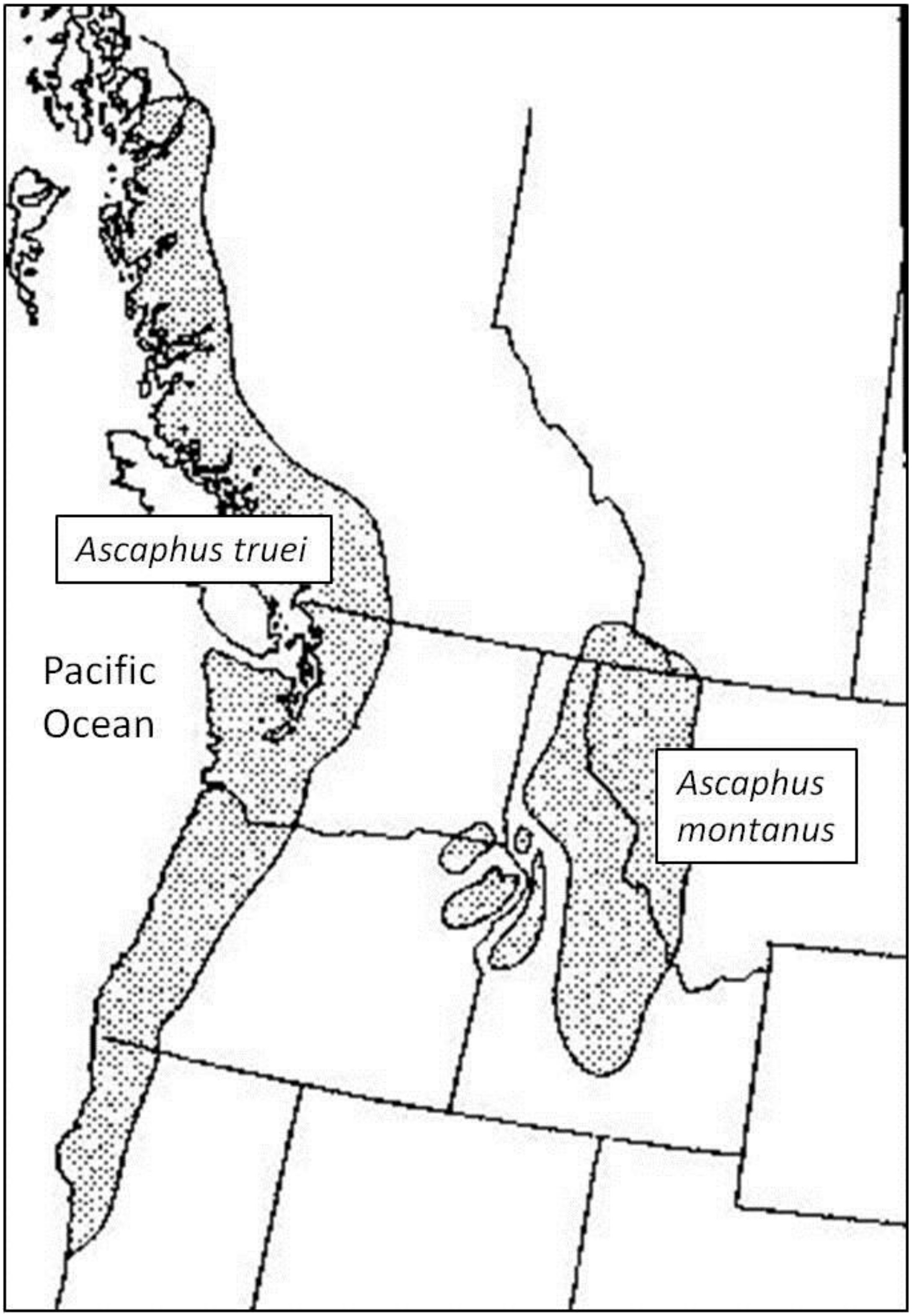

FIGURE 3. The geographic distribution of the two tailed frog species (stippled) in the PNW (adapted from Nielsen *et al.* [2001]).

Boundaries lines between Canadian provinces and US states are indicated.

further easterly position. Dupuis and colleagues (2000) attributed this pattern to fewer small streams, many of which freeze in winter (see THE OVERWINTERING SEASON subsection within the LIFE HISTORY section), and further indicated that *A. truei* appears to be present in areas where the snow blanket is sufficient to maintain flowing water through the winter. This pattern may also help explain why *A. truei* are relatively rare east of the Cascade Mountains in Washington, although the dearth of mesic stream-edge habitat as one moves south may also contribute to this pattern.

Based on data collected in 1995-1998, the known northern limit of *A. truei* distribution is the near northwest margin of Kitsumkalum[19] Lake (about 54.80°N latitude), south of the Nass River, British Columbia (Dupuis *et al.* 2000). The extent of tailed frog range in this area is poorly defined because of the remote nature of the region; surveys for the species were limited to areas with fly-in access and permanent streams that could be reached by logging road. Moreover, the survey approach was limited to one 20-min time-constrained search for which *A. truei* detection probabilities and false negative error rates are unknown. Dupuis and colleagues (2000) found *A. truei* in only 15 of the 110 streams surveyed across this region. Besides the surveys conducted for *A. truei* in the Nass system and northward that revealed no detections, inquiries with individuals with field experience regarding its potential presence in the nearby Alaskan panhandle also failed to reveal evidence that the species might be present (Dupuis *et al.* 2000).

Based on one *A. truei* collected on 20 June 1951, the southern limit of distribution is in Russian Gulch State Park, Mendocino County, California (about 39.33°N latitude; Salt 1952). This locality, 2.4 km (1.5 mi) straight-line distance from the coast, is a damp steep canyon heavily forested with Coast Redwood (*Sequoia sempervirens*) and Douglas-fir (*Pseudotsuga menziesii*). Salt (1952) commented that, "Since streams similar in character to Russian Gulch occur in the redwood forest to the south as well as to the north, it is not unlikely that the limit for the species lies even farther to the south, perhaps even in the coastal portion of central Sonoma County." However, no more southerly records have been found in this highly accessible region. Central Mendocino County represents the southern limit of several species at an apparent tectonic boundary (e.g., Shaffer *et al.* 2004). The southern limit of *A. truei* may also end at this boundary.

The range of *A. truei* expands east in northern Washington (Dvornich *et al.* 1997) and southern British Columbia (Mallory 2004). The easternmost records are from the Okanogan in north-central Washington, about 120.13°W longitude (Dvornich *et al.* 1997). The westernmost records, on islands of the mid- and northern coast of British Columbia (Princess Royal and Gribbell[20] Islands at the mouth of Douglas Channel, 129.1-128.5°W longitude; Dupuis *et al.* 2000) are near the northern limit of the range because the British Columbia coastline stretches westward with increasing latitude.

Ascaphus montanus: The range of *A. montanus* encompasses the interior portion of the range of tailed frogs in the states of Idaho, Montana, Oregon, and Washington; and the province of British Columbia (Adams and Pearl 2005b; FIGURE 3). Anthony Russell and Aaron Bauer (2000) speculated that tailed frogs[21] might also occur in Waterton

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[19] Kitsemkalum Lake that Dupuis and colleagues (2000) recorded is an emendation of Kitsumkalum Lake.

[20] Gribbell Island is the Gribble Island of Dupuis and colleagues (2000).

[21] The Russell and Bauer (2000) compendium of the Alberta herpetofauna predates Nielson and colleagues (2001) partitioning of the two tailed frog species, but if tailed frogs occur in Alberta, they would likely be *A. montanus*.

Lakes National Park and near Castle River in the extreme southwest corner of the province of Alberta (Canada) based on known localities in the Flathead River system (in British Columbia) and Glacier National Park (Montana), both located within 25 km (16 mi) of Alberta. This supposition remains unverified. In a near parallel fashion to *A. truei* distribution in the coastal mountains, most of the range of *A. montanus* occurs west of the continental divide (Werner *et al.* 2004). A few localities exist east of the divide in mid-western Montana (Donaldson 1934; Werner *et al.* 2004). Notably, these records are also near low points in the divide. For example, the record from Midvale Creek (Donaldson 1934) is about 10 km (6 mi) east of Marias (or Roosevelt) Pass (1,591 m [5,220 ft]), the lowest pass on the continental divide over the known range of *A. montanus*. Similar to *A. truei* in coastal mountain ranges, the west side of continental divide, which receives greater moisture, seems to influence the macro-distribution of *A. montanus*. Unlike *A. truei*, which has near continuous distribution in the Cascades and coastal mountains toward the southern end of its range, the canyon of the Snake River and some of its tributaries fragment the southwestern distribution of *A. montanus* (Nielson *et al.* 2006). Prominent among these isolated fragments is the Blue-Wallowa Mountain complex of southeast Washington/northeast Oregon (Bull and Carter 1996a, Nielson *et al.* 2006).

The precise northern limit of *A. montanus* has not been formally identified (see discussion of *A. montanus* range in British Columbia [Mallory 2004; see also Dupuis *et al.* 2000]), but is described as being within 20 km (12.5 mi) of the Canada-United States border (Dupuis and Wilson 1999). Existing range maps (Dupuis *et al.* 2000, Mallory 2004) reveal a similar northern limit for each of the two northernmost extensions of *A. montanus* range into British Columbia, located in the Columbia Ranges and the Rocky Mountain foothills. Twenty kilometers north of the international border is about 49.17°N latitude.

Though the precise southern limit of *A. montanus* has also never been formally identified, it is likely near the Boise Mountains locality that Nielson and colleagues (2006) report from south-central Idaho, i.e., on an unnamed tributary of the Middle Fork Boise River near Rocky Bar (roughly 43.68°N latitude).

Additional unverified reports of tailed frogs exist for the Ochoco Mountains of central Oregon (Stebbins 2003), and Corkran and Thoms (2006) mapped this region in the distribution of *A. montanus*. If tailed frogs from this region are really *A. montanus* (its mapped location is roughly equidistant from the ranges of *A. truei* in the Cascade Mountains and that of *A. montanus* in the Blue-Wallowa Mountain complex), then these observations represent the easternmost records for the species.

Elevational Range: The elevational range of tailed frogs in North America extends from near sea level (based on several records in their coastal range; California: 3 m [10 ft], Bury 1968; British Columbia: <30 m [<100 ft], Carl and Cowan 1945; see also Jones *et al.* 2005; Corkran and Thoms 2006) to 2,557 m (8,390 ft) in the Bitteroot Mountains of Montana (Werner *et al.* 2004).

Ascaphus truei: The elevational range of *Ascaphus truei* extends from near sea level (several records; see above) to 1,981 m [6,500 ft] on Pony Mountain, Trinity County, California (Bury 1968; *contra* Brown 2005).[22] Though no one has determined whether *A. truei* exhibits an elevational cline with latitude (e.g., decreasing elevation with increasing latitude), what are presumed to be upper elevation records imply such a cline exists. In British Columbia, *A. truei* extends to 1,800 m (5,905 ft) in the subalpine zone of the Okanagan Cascades (Gyug 2001; K. Paige, 2014, pers. comm.). An upper elevation limit for *A. truei* in Oregon and Washington is has not been systematically explored (R. Bury, 2014, pers. comm.).

Ascaphus montanus: No rangewide lower elevation limit has been reported for *A. montanus*, but that limit is likely at intermediate elevations because habitat becomes less suitable as elevation decreases in the interior west. Franz and Lee (1970) sampled[23] 74 sites for *A. montanus* across the Flathead River drainage of northwestern Montana between 792 m (2,600 ft) and 1,920 m (6,300 ft), but recorded no *A. montanus* at sites lower than 884 m (2,900 ft). Resolution of this lower limit may be poor as only 5 streams below 914 m (3,000 ft) were sampled. Franz and Lee (1970) felt that *A. montanus* disappeared below elevations around 914 m (3,000 ft) in the Flathead system largely because stream gradients decreased markedly at that point – as upslope areas transition to valley floors. Maughan and colleagues (1980), who reported on its regional distribution in the Clearwater River drainages in north-central Idaho, stated that nearly all populations were recorded over 975 m (3,200 ft),[24] though they could not explain why. In British Columbia, Dupuis and colleagues (2000) reported *A. montanus* down to 1,200 m (3,937 ft), which is also close to the general elevation at which marked changes in stream gradient occurs between upslope areas and valley floors in Canada.

Summarizing the distribution of *A. montanus* in Montana, Werner and colleagues (2004) provided the uppermost known elevation for the species at 2,557 m (8,390 ft) in the southern Bitterroot Mountains (Ravalli County). In British Columbia, *A. montanus* is reported as occurring up to 1,905 m (6,250 ft) in elevation (Sutherland 2000) based on data originally collected by Dupuis and colleagues (2000). In their guide to amphibians of Oregon, Washington, and British Columbia, Corkran and Thoms (2006) reported tailed frogs up to 2,140 m (7,021 ft); this record reflects the upper limit of *A. montanus* in the Wallowa Mountains. The upper elevation record for British Columbia is lower than the records for Montana and Oregon, suggesting that there may be a cline similar to the one suggested for *A. truei*.

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[22] Brown (2005) reported the upper elevation limit of *A. truei* as 1,600 m [5,249 ft] in Mount Rainier National Park. Corkran and Thoms (2006) report an upper elevation limit of 2,140 m [7,021 ft], but their data represent a composite of information on *A. truei* and *A. montanus,* that upper elevation limit is the elevation record for *A. montanus* that was known at that time.

[23] Franz and Lee (1970) did not specify reach lengths sampled. They focused on larvae due to their greater detectability and used several techniques, but only a rubble rousing-like technique was described. Headlamp-assisted night searches along streams were the focal method for obtaining adults.

[24] Most collections were made with backpack electrofishing units, but kicknet sampling was also used (Maughan 1972, Maughan *et al.* 1980).

Landscape-Level Occupancy: Patterns of tailed frog occupancy across landscapes are difficult to infer due largely to differences among sampling designs. These differences include but are not limited to the length, frequency, and seasonality of surveys; the mode of sampling (especially where detectability may change); and differences in accessibility among sites.

Ascaphus truei: Welsh (1990) conducted the first study that provided some data on the landscape distribution of *A. truei*. He selected 93 sites from the Douglas-fir-dominated mixed coniferous hardwood forests of northwestern California and southwestern Oregon. With exceptions, sites were located in three areas: the upper Illinois/upper Smith Rivers near Oregon/California boundary, the middle Prairie Creek/Trinity River area in the vicinity of Willow Creek (town), and the upper Mattole River area near Branscomb.[25] Sites were selected from young, mature, and old forests based on stand characteristics (Franklin *et al*. 1986), but the selection frame was not specified.[26] Of 93 sites, 54 were upslope (i.e., did not contain a stream) and ranged in size from 21 to 150 ha, and 39 were streams in second- or third-order basins. As this study addressed the entire herpetofaunal assemblage, three sampling approaches were used: pitfall traps, time-constrained searches, and area-constrained searches.[27] Only the area-constrained searches in streams yielded *A. truei* in numbers sufficient for analysis. For streams sampled in this manner, Welsh (1990) reported significant differences in the levels at which tailed frogs were detected among the three forest age categories: 11% (n = 1) of 9 young sites, 56% (n = 5) of 9 mature sites, and 81% (n = 17) of 21 old-growth sites; a finding later repeated from a slightly different perspective (Welsh and Lind 1991).

Assuming Welsh's unexplained sampling frame for site selection is not problematic, that smaller sample sizes in the two younger forest age categories did not compromise his study, and that detection of tailed frog across forest age categories was unbiased, Welsh (1990) showed an increase in *A. truei* occupancy with forest age in the southern portion of *A. truei* geographic range.

In characterizing the terrestrial amphibian assemblage in the Oregon Coast Range, Corn and Bury (1991) studied stands in an age sequence ranging from recently harvested to old-growth.[28] The 27 old-growth stands sampled were also grouped into wet (n = 5),

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[25] Eleven (12%) of the 93 sites used in this study were located outside of those three general areas.

[26] Based on tree ring counts, sites were grouped into three age classes: young (<100 years old), mature (100-200 years old), and old-growth (>200 years old). Four sites that met the criteria for old-growth based on the number of large trees, snags, and logs (Franklin et al. 1986) but were <200 years old were included in old-growth.

[27] Forty-nine (91%) of the 54 terrestrial sites had a grid of 36 pitfall traps in a 6 × 6 square arrangement with 15-m spacing between traps. Traps, which consisted of taped tin cans buried flush to ground level and concealed by wood cover, were opened 50 nights in fall (October and November) 1984, and 30 nights in fall (October) 1985. Time-constrained surveys (TCS) used 2-3 surveyors moving through sites for 4 hours during which time all microhabitats were searched; the latter included raking litter with a potato rake, turning rocks and small logs, breaking open larger decaying logs, and probing vegetation. TCS surveys were done at all 54 terrestrial sites during April-June in each of 1984 and 1985. Area-constrained searches were conducted in three 5-m reaches in each stream surveyed. Welsh (1990) selected the starting point for the first reach 50 m upstream from the nearest trail or road access, second and third reaches were spaced 50 m upstream from the upper end of the first and second reaches, respectively. Each reach was searched by "moving all rocks where possible" and "working upstream with catch nets placed downstream to captured dislodged animals" (Welsh 1990).

[28] Corn and Bury (1991) initially selected stands to conform to a chronosequence of four categories: recently harvested (<10 yrs; n = 5), young (40-75 yrs; n = 8), mature (80-120 yrs; n = 10) and old-growth (150-525 yrs; n = 27). Most stands were on the interior or the eastern flank of the Coast Range, and land management of these stands including the BLM, Forest Service, and the city of Corvallis. Only three of the five recently harvest stands were monitored with pitfall trap arrays.

moderate (n = 14), or dry (n = 8) moisture categories.[29] Sampling was pitfall trap-based.[30] *Ascaphus truei* was not found in the dry old-growth stands or the three recently harvested stands sampled. Pitfalls captured only post-metamorphic *A. truei*, so as Corn and Bury (1991) noted, proximity to breeding habitat, in the case of *A. truei* – streams, limited the ability of this study to identify patterns. They did comment that most pitfall grids were located within a few hundred meters of a perennial stream, but occupancy of *A. truei* was not related perennial stream proximity.

Based on a two-year study across the Blue River watershed (central western Oregon), Hunter (1998) was the first to provide a detailed landscape analysis of the distribution of *A. truei*, though his study actually addressed all stream-associated amphibians. In 1995, he stratified the watershed by subdrainage and elevation into 36 units, in each of which he sampled three to six 5-m (16-ft) reaches.[31] Selection of 5-m (16-ft) reaches was non-random based on topography indicating a functional stream channel, and a preference for accessible and first- and second-order streams. In 1996, he modified his selection process into a three-tiered stratified random approach,[32] eliminating the non-random step. At the time of his work, about one-third of the Blue River watershed had been harvested for timber, but the selection process was not stratified on whether harvest had taken place. Data from each year were spatially exclusive, and in the analysis, Hunter (1998) combined all 273 5-m (16-ft) reaches, and treated larval and metamorphosed[33] life stages separately. Larval *A. truei* were detected in only 8% (21 of 273) of 5-m (16-ft) reaches. Hunter did not detect larval *A. truei* in the smallest streams and rarely found them in the largest ones. His modeling revealed that the greatest likelihood of larval *A. truei* occurrence was in moderate-sized streams, which was represented by a quadratic relationship to basin size ($P = 0.0007$). In contrast, Hunter detected metamorphosed *A. truei* in 23% (62 of 273) of 5-m (16-ft) reaches, but could not discern a clear trend in their occurrence across basin sizes. However, he did find that over the 394-1,453 m (1,293-4,767 ft) elevational range sampled, the likelihood of metamorphosed *A. truei* occurrence increased significantly with elevation ($P < 0.001$). For every 100-m increase in elevation, the odds of occurrence increased ×1.52. The only other landscape-level variable with a significant trend for metamorphosed *A. truei* was slope ($P = 0.003$).[34] For every 10% increase in slope, the odds of occurrence increased ×1.52.

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[29] The categories were wet, moderate, and dry (Corn and Bury 1991). Moisture category was based on a multivariate ordination of understory vegetation (Spies and Franklin 1991).

[30] Pitfall traps were installed in 6 × 6 grid arrays with 15 m inter-trap spacing in each stand. Bury and Corn (1987) provided details of trap construction and installation

[31] The primary mode of detecting amphibians was visual. In 1995, in portions of the stream with non-turbulent water, Hunter (1998) probed, moved, or removed the substrate to locate concealed amphibians, which were then coaxed into a dipnet. In turbulent water, a net was set downstream of the target reach, its substrate was disturbed, and dislodged animals either captured directly or washed into the net. Search was conducted until sand-sized or smaller particles were dominant or filled available interstices. In 1996, searches were similar except that a net was placed across the entire wetted channel at the downstream end of all 5-m reach sampled.

[32] This approach was a serial random selection, first from a grid of 287 1-km^2 squares overlain on the watershed; and second from the 100 1-ha units within each randomly selected 1-km^2 square. Within each 1-ha units, three or four points at the intersection of 100-m^2 squares were randomly selected from the 100 within each randomly selected 1-ha unit. The stream channel closest to these randomly selected points was chosen to place a 5-m sample reach.

[33] Individuals in the process of transformation (metamorphosis) were included in analysis of the larval form. Metamorphosed animals included all life stages after metamorphosis.

[34] Slope was measured as 1-km resolution using GIS and the slope range across study sites was 24-64% (Hunter 1998).

In a four-year study (1993-1996), Diller and Wallace (1999) assessed the distribution of *A. truei* in the managed forest headwater landscape of northwestern California. They selected 72 sections in a stratified random approach that chose up to four sections per township.[35] They sampled the first second-order stream encountered along the major road through each section that had at least 1,000 m (3,281 ft) of channel with flowing water. The study area consisted of second- and third-growth forests with a zero-to-80-year stand age range. They grouped the 13 lithologies recorded across this landscape into consolidated and unconsolidated categories.[36] Larval tailed frogs, indicative of instream reproduction, were detected in 54 (75%) of the 72 streams sampled. Streams having consolidated lithologies represented 93% (n = 67) of sampled streams, and all streams where larval tailed frogs were found had consolidated lithologies, a significant difference ($P < 0.001$). The only other landscape-level variable that revealed significant patterns was stand age. The median age of forest stands surrounding sites at which *A. truei* was found was significantly younger (median [$\tilde{x}$] = 32 yrs, range = 0-84 yrs, n = 54) than the median age greater of stands surrounding sites without *A. truei* ($\tilde{x}$ = 39.5 years, range = 8-117 yrs, n = 18; $P = 0.051$). Diller and Wallace (1999) explained the inverse relationship between *A. truei* occupancy and stand age based on the historically pattern of harvesting and coastal lithology in coastal California. Stands closest to the coast were harvested first and that is also where unconsolidated lithologies were likely to be encountered. The more interior steeper sites having shallow rocky soils characteristic of consolidated lithologies were harvested more recently. Hence, the oldest second growth tended to be in areas that had lithologies unsuitable tailed frogs.

A second two-year study also conducted in 1995-1996 evaluated amphibian occurrence on perennial non-fish-bearing streams on ~5,000 ha (12,350 ac) of industrial forestland in southwest Washington (Wilkins and Peterson 2000). The 40 sites in this study were stratified among two major lithologies (marine sediment and basalt) and the eight major stream basins in this landscape. Stratification of selection in the latter was in proportion to their perennial non-fish-bearing channel length. Twenty sites (9 basalt and 11 marine sediment) were sampled each year. To reduce undesired variability, selection was also confined to streams in near rotation age (50-65 years old) second-growth stands, and road crossings and tributary junctions were avoided[37]. Wilkins and Peterson (2000) defined a 100-m (328-ft) channel unit upstream from an arbitrary point at each site, and generally sampled a 5-m (16-ft) reach that began at the downstream boundary of each third of this unit.[38] Before sampling, the ends of each 5-m (16-ft) reach were blocked off with screening. During the search for amphibians, all cover objects >5 cm (2 in) in diameter were removed from the channel and finer substrates were hand sifted. *Ascaphus truei* (all larvae) were recorded in only 13% (n = 5) of 40 of these non-fish-bearing streams. All sites at which *A. truei* were detected were on a basalt lithology,

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[35] The number of sections per township was reduced if the study area (i.e., Simpson Timber Company [now Green Diamond] ownership) was not located in the entire township.

[36] The consolidated geologic category consisted of older formations that form boulders, cobbles, and gravel during decomposition into fine sediments, whereas the unconsolidated category included younger marine deposits that decompose directly into silt and sand (Diller and Wallace 1999).

[37] Wilkins and Peterson (2000) avoided placing channel units extending within 200 m downstream and within 100 m upstream of road crossings, and they shifted sampling upstream where tributary junctions fell within a channel unit.

[38] A physical obstruction sometimes forced shifting the placement of 5-m reaches within the channel unit. As a consequence, spacing between 5-m reaches ranged from 20 m to 65 m.

which represented 28% of the 18 basalt sites.

Dupuis and colleagues (2000) sampled 303 streams in north (n = 110), mid- (n = 100), and south (n = 93) coastal British Columbia using 20-min time-constrained survey (TCS) approach over three different years (1995, 1996, and 1998). Sampled streams were assumed to be permanent (= perennial) on the basis of the presence of water on the sample date; absence of *A. truei* was assumed if no detections were made within the 20-min search interval. The remote nature of north and mid-coastal regions restricted entry to flying into active logging camps, and the sampling frame to road-accessible permanent streams (as defined above) within range of these camps. In contrast, the south coastal region was directly road-accessible. Given these limitations, *A. truei* was detected in 17 (15%), 36 (36%), and 43 (54%) streams in north, mid-, and south coastal areas, respectively. If one assumes that detectability was uniform across sampled areas, then *A. truei* occupancy may decrease with increasing latitude. How the pronounced accessibility differences between south coastal and north and mid-coastal regions may influence these estimates is unknown.

Working on the Olympic Peninsula, Adams and Bury (2002) surveyed 163 headwater streams in 12 of the 13 major drainages in Olympic National Park.[39] Each stream was sampled once in the June-August interval over the three years 1996-1998. Within a sampling frame restricted to streams intersected by main trails or roads, they randomly selected one-third to one-half of the small (depth ≤30 cm [12 in]) perennial streams in each major drainage.[40] They sampled 10 1-m (3.3 ft) segments over 100 m (328 ft) beginning 30 m [100 ft] upstream of trail or road crossings. Sampling consisted of a light-touch search where a net was placed immediately downstream from rocks and debris that was overturned to captured dislodged amphibians. The analyses of Adams and Bury (2002) focused on examining patterns of relative abundance, but they reported selected findings on occupancy. They detected *A. truei* in 56% of surveyed streams, which were categorized as having either consolidated or unconsolidated substrates.[41] In particular, they found *A. truei* in six of nine (67%) streams with consolidated substrates and 86 of 154 (56%) streams with unconsolidated substrates. Adams and Bury (2002) did not statistically contrast the proportion of *A. truei*-occupied sites between the two substrate categories, but these percentages are likely not significantly different.[42] Adams and Bury (2002) also briefly commented on the higher occupancy of *A. truei* they found on unconsolidated substrates than in other studies on done managed forest landscapes, namely, those of Diller and Wallace (1999) and Wilkins and Peterson (2000), attributing the lower occupancy to forest practices. Forest practices might explain the difference, but two conditions potentially confound it. First, strong asymmetry exists in what was included in the unconsolidated substrate category among the three studies and one or more co-variates linked to latitude likely influence a gradient in the level of occupancy.

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[39] Adams and Bury (2002) reported 141 streams in their method, but this was the number of streams used in the relative abundance (density) analysis, not the total number of streams used in the occupancy comparisons listed in Table 4 (M. Adams, 2014, pers. comm.).

[40] Surveyed streams were generally ≥50 m apart and considered to be independent (Adams and Bury 2002).

[41] This was general categorization of surface lithology (described by Adams and Bury [2002] as surface geology, where consolidated substrates were basalt and unconsolidated substrates were mainly marine sediments.

[42] At an $\propto$ of 0.05, the lower and upper 95% confidence intervals on the binomial distribution for 67% on consolidated substrates was 29.9% and 92.5%; the same for the 56% on unconsolidated substrates was 47.1% and 64.5%.

On the east slope of the Oregon Coast Range, Stoddard and Hayes (2005) randomly selected 16 third-order basins from the Bureau of Land Management (BLM)-managed landscape[43] to characterize the relationships of stream-associated amphibians, including *A. truei*, at three spatial scales: 1) the third-order drainage scale, 2) a forest stand (of similar age) scale within each third-order basin (termed patches), and 3) 2-m (6.6 ft) stream reach scale within those patches. They sampled amphibians in 35-50 randomly selected 2-m (6.6 ft) stream reaches in each third-order basin.[44] Habitat variables were also sampled at all three scales.[45] Using an AIC-based analysis, Stoddard and Hayes (2005) generated logistic regression models for the occurrence of larval and post-metamorphic *A. truei*[46] at all three scales, but only drainage and patch scales provided landscape-level data. At the drainage scale, the best models predicting the occurrence of larval or post-metamorphic *A. truei* had only one variable, a forested riparian management zone (RMZ), with which a positive relationship existed. The only other *A. truei* model with enough support to be contending ($\Delta < 2$)[47] was a larval model that included both the positive relationship with forested riparian stand presence and a negative relationship with over 60 percent side slope gradient. Furthermore, each 10 percent increase in stream length with a >46-m (150 ft) RMZ increased odds of larval and post-metamorphic *A. truei* occurrence by 24 and 27 percent,[48] respectively. Across the range of RMZs studied, odds of occurrence roughly doubled with an increase of 30 percent in stream length with an RMZ. However, as Stoddard and Hayes (2005) emphasized, probability of occurrence was low for larval and post-metamorphic tailed frogs; in particular, when RMZs bordered 30 percent of the stream length, the probability of occurrence for *A. truei* larvae and post-metamorphs was 0.12 and 0.03,

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[43] Stoddard and Hayes (2005) selected from all third-order drainages in the Eugene and Salem Districts of the BLM on the east slope of the Oregon Coast Range. They stratified drainages into low, moderate, and high intensity forest management categories based on the percentage of forest <26 and >55 years old in each drainage. In low intensity drainages, <30% of forests were <26 years old and >60% were >55 years old. In moderate intensity drainages, 40–60% of forests were <26 years old and 40–60% were >55 years old. At least 60% of forests in high intensity drainages were <26 years old and <30% were >55 years old. In all categories, <10% of the area was composed of forest 26–55 years old. We randomly selected five high-, five moderate-, and six low-intensity drainages for study. Study drainages ranged from 94 to 197 ha in area and 205 to 662 m in mid-drainage elevation.

[44] Stoddard and Hayes (2005) sampled June-August 1998 and June-September 1999. Three to four third-order drainages, grouped by proximity, were sampled weekly. The field season had early and late periods in 1998; early, middle, and late periods in 1999; a random group of drainages was sampled weekly, and each drainages was sampled once in each period. Each 2-m stream reach was sampled only once. After capturing amphibians in a visual search, one surveyor searched beneath undercut banks, movable rocks and coarse wood, using a dip net to capture animals.

[45] Drainage-scale habitat variables were: 1) age structure of drainage as the ratio of the area of <15- to >15-year-old forest; 2) road density as the ratio of road length to drainage area (range 8-34 m/ha), 3) slope stability as the percent of drainage area with side slopes >60% (range 1-43%); and 4) the proportion of stream length with RMZs >46 m wide on both stream margins and >55 years old (range 5–100%). Patch-scale variables were: 1) placement into one of eight groupings via digital imaging to identify whether RMZs >55 years old occurred <15 m, 15–30 m, 30–46 m, and >46 m on each side of the stream; 2) a heat index (0 to 1 scale) derived from the averaged aspects of 2-m reaches in each patch and transformed into a heat load index (Beers et al.1966); 3) gradient calculated from a 10-m DEM averaged over the sample units in each patch; and 4) clinometer-measured side-slopes averaged over the sample units in each patch. Reach-scale variables were: 1) percentage of slow (pool and glide) and fast (riffle and cascade) water, and slow:fast ratios; 2) percent cover of rock substrates; 3) the ratio of rock substrates with little or no cover value (bedrock and particle size <32 mm in maximum length) to substrates with greater cover value (particle size >32 mm in maximum length) to index substrate condition; 4) stream width; 5) proportion of undercut bank; 6) percent cover of coarse wood; 6) percent cover of overstory trees and shrubs; and 7) elevation.

[46] Stoddard and Hayes (2005) termed non-larval tailed frogs adults; these actually represent juveniles and adults.

[47] Δ is the difference between the Akaike Information Criterion value for a given model and that of the model with the greatest empirical support.

[48] The 95% confidence intervals (CI) on odds of occurrence for larval and adult *A. truei* were 12-38% and 11-44%.

respectively. At a patch scale, the best model for predicting the occurrence of post-metamorphic *A. truei* was identical to the best drainage-scale model. However, the two-variable model involving a positive relationship between occurrence and each of RMZ presence and gradient had a nearly identical level of empirical support ($\Delta = 0.02$). The best larval patch-scale model had three variables that involved negative relationships with each of stream gradient and heat load index (see footnote 45), and either a positive or negative relationship with stand age.[49] Similarly, the two-variable model with only the heat load index and stand age variables had nearly the identical level of empirical support ($\Delta = 0.01$). Stoddard and Hayes (2005) also found that the likelihood of finding *A. truei* in streams at the patch scale increased with greater RMZ width. The odds of finding larval *A. truei* in a stream with RMZs >46 m (150 ft) wide were roughly five times that of the odds of finding larval *A. truei* in a stream with stands <15 m (50 ft) wide. The odds of larval *A. truei* occurring in streams with RMZs either <15 m (50 ft) or 15-30 m (50-100 ft) wide differed from the odds of larval *A. truei* occurring in streams with RMZs >46 m (150 ft) wide.[50] For adult tailed frogs, only odds of occurrence in streams with RMZs <15 m (50 ft) wide differed from the odds of occurrence in streams with RMZs >46 m (150 ft) wide,[51] but comparison to RMZs 30-46 m (50-100 ft) wide could not be made since adult tailed frogs were not detected in streams with RMZs in this width range. Lastly, Stoddard and Hayes (2005) noted that at the patch scale, side slope and stream gradients did not differ among streams with different RMZs widths, suggesting the odds ratios on *A. truei* probability of occurrence reflect influences of the width of RMZs, not the other habitat characteristics they measured. The importance of the Stoddard and Hayes (2005) study was that it provided the first empirical evidence that riparian forest stands or RMZs width could substantially influence *A. truei* occupancy. However, whether actual thresholds in RMZ width exist that influence *A. truei* occupancy remains unclear.

In southwestern Washington, Hayes and colleagues (2006) sampled two sets of non-fish-bearing basins from the managed forest landscape of the Stillman Creek watershed, a Chehalis River tributary. An initial set of 81 basins was sampled over three years (2000-2002) during the August-October interval. A longitudinal light-touch approach (Quinn *et al.* 2007) was used to sample the dominant thread of each stream from the previously electrofish-determined last fish point to the upstream origin of the stream. The dominant stream thread contributes the most water to the system and was determined by following the stream segment with the most flow at each tributary junction. This initial effort revealed little evidence of *A. truei* reproduction (as assessed by larval presence) in small non-fish-bearing basins. However, stream selection had been randomized on road crossings and selection based on road crossing biased against the selection of very small basins (that is, the likelihood of a road crossing a basin decreased with basin size). Hence, if the presence of a road crossing altered the

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[49] Stand age was classified into eight categories depending on whether one or both banks of a stream had stands falling to four categories: 0-15, 15-55, 56-105 or >105 years of age. Both banks with a stand age of >105 years was the reference category. Regression co-efficients for larval *A. truei* for the seven other categories were: 1) both banks 0-15 = -1.60; 2) 0-15, 15-55 = -0.72; 3) 0-15, >55 = -0.27; 4) both banks 16-55 = -2.05; 5) 16-55, >55 = -0.70; 6) both banks 56-105 = -0.23; and 7) 56-105, >105 = 1.03.

[50] Stoddard and Hayes (2005) found that for RMZs <15 m wide, $\chi^2 = 22.26$, $P = 0.0001$; for 15–30 m, $\chi^2 = 7.07$, $P = 0.0078$.

[51] Chi-square = 4.56, $P = 0.0328$.

likelihood of *A. truei* occupancy, an observation of reduced occupancy in small non-fish-bearing basins would be biased. For this reason, Hayes and colleagues (2006) sampled a second set of 65 basins randomly selected from electrofish-determined last fish points, the criterion used to delimit non-fish-bearing basins. The dominant thread of each stream was sampled using the same approach over two years (2003 and 2005). The results of this effort revealed an identical pattern of reduced *A. truei* occupancy on small non-fish-bearing basins, and in particular, lack of any evidence of reproduction in 1st-order basins. As 1st-order basins had almost no surface flow during the summer low flow period (15 July–30 September), Hayes and colleagues (2006) concluded that *A. truei* lacked the habitat to reproduce in these small basins. This study used single pass sampling, which would potentially underestimate occupancy, but sampling of the entire length of the dominant thread reduces the likelihood that this bias was significant.

In a broader regional study, Kroll and colleagues (2008) sampled 141 perennial non-fish-bearing streams from the commercial forest landscape in western Oregon and Washington from July to October 2006. They randomly selected sample sites from all perennially flowing non-fish-bearing streams on participating ownerships. Forest stand ages ranged from 0-106 years ($\bar{x}$ = 35, SE = 5). Similar to Hunter (1998), they sampled all stream-associated amphibian species. Kroll and colleagues (2008) used removal sampling (MacKenzie *et al.* 2006) in which 100-m (328-ft) reaches were visited up to three times over intervals of 4-16 days between visits.[52] If all three stream-associated study species were found during the first or second visit, that stream reach was removed from further sampling. To ensure independence, sample reaches were always located in different fourth-order basins.[53] A modified form of longitudinal light-touch sampling (Quinn *et al.* 2007) was used; all cover objects <30 cm in diameter except coarse woody debris were moved[54] and replaced in their original positions during searches. This regime resulted in Kroll and colleagues (2008) sampling 100 reaches three times, 8 reaches twice, and 33 reaches once. *Ascaphus truei* were detected on the first visit to 41 of the 52 streams in which the species was ultimately detected over the course of the study (i.e., in the second or third visit). *A. truei* occupancy was modeled from data on a total of 133 of these reaches. None of the covariates Kroll and colleagues (2008) assessed to determine whether they might affect detection probability received strong support.[55] Their estimates of *A. truei* detection probability declined from 0.78 to 0.43 over the sampling season so they used a model incorporating date as the basis against which to assess alternative occupancy models. The landscape occupancy pattern Kroll and colleagues (2008) identified for *A. truei* was a quadratic relationship with bankfull width regardless of interacting factors (e.g., crayfish presence). Bankfull width is correlated with basin size (Kroll *et al.* 2008), so this pattern agrees with the work of Hunter (1998). However, the real importance of the study was estimating detection probability, which previous studies assumed either did not vary or differ from 1. In other words, occupancy probabilities of *A. truei* would have been underestimated if individual streams had been sampled only once or twice.

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[52] Kroll and colleagues (2008) generally sampled a continuous 100-m reach, but if large logs or other obstructions that obscured the streambed prevented surveying a portion of the stream, an equivalent distance upstream was added.

[53] Fourth-order based on the Strahler (1951).

[54] All coarse woody debris was left undisturbed.

[55] Covariates examined included Julian date, time of day, rain during the survey, rain within a 24-h period before the survey, cloud cover or sunshine, and water and air temperature.

In a second regional study in 2007-2008, Kroll and colleagues (2010) sampled 70 randomly selected third-order basins in western Oregon and Washington. They again used the light-touch survey approach and surveyed six 100-m (328 ft) segments in each third-order basin.[56] As with Kroll and colleagues (2008), removal sampling was used (MacKenzie *et al.* 2006) until all target taxa (all stream-associated amphibians were sampled) were detected or two surveys were completed. They detected *A. truei* in 38 of 67 (57%) basins.[57] They also detected *A. truei* in six of 18 (33%) of basins <50 ha [124 ac], 12 of 21 (57%) of basins 50-100 ha [124-247 ha] and 20 of 28 basins (70%) of basins >50 ha [124 ac]. These results run counter to the quadratic pattern reported by Kroll and colleagues (2008), but agree with occupancy declines at smaller basin sizes. Further, *A. truei* occupancy probability was estimated at 0.60 (95% CI = 0.46-0.72) and was inversely related to site index, a productivity measure, for each basin.[58] Though not reported, site index varied geographically in a way consistent with productivity (A. Kroll, 2014, pers. comm.), though as Kroll and colleagues (2010) indicated, it may not reliably index in-stream productivity where much of the stream length is buffered.

In summary, available data suggest that *A. truei* occupancy varies with basin size. The seemingly conflicting information between the quadratic (Hunter 1998, Kroll *et al.* 2008) and linear (Hayes *et al.* 2006, Kroll *et al.* 2010) patterns in occupancy reported may simply reflect restriction of the first of the latter studies to non-fish-bearing basins on intrusive basalt substrates that were size-limited due to their geographic location and the second of the latter studies encompassing both a broad range of lithologies and fish- and non-fish-bearing streams.[59] A decrease in occupancy near headwaters may reflect lack of breeding and rearing habitat as a result of less reliable perennial aquatic habitat (Hunter 1998, Hayes *et al.* 2006, Kroll *et al.* 2008), whereas decrease in occupancy at larger stream sizes may reflect a potential negative interaction with fishes (Hunter 1998), stream conditions (e.g., higher flows) less favorable for rearing (Kroll *et al.* 2008), or a combination of these. Earlier studies probably underestimated landscape-level occupancy because they relied on single-pass sampling that prevents estimating detection probability. Small sampling units (5 m [16 ft; Hunter 1998] to three 5-m (16-ft] units [Wilkins and Peterson 2000]) or a relatively limited effort (20 min time-constrained searches [Dupuis *et al.* 2000]) may also contribute to underestimating occupancy.[60]

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[56] Kroll and colleagues (2010) placed one segment in the 3rd-order reach below the 2nd-order confluence, two segments in 2nd-order streams immediately above the confluence with the 3rd-order channel, and three segments in 1st-order streams immediate above the 2nd-order confluence. However, because the number of possible 1st- and 2nd-order reaches could be, respectively, more than three or two, the reaches in which sampling segments were placed were randomly selected where these were more numerous. For each 100-m segment, searches were constrained to 2.5 hrs or two individuals searching for 1.25 hrs.

[57] Three basins were conservatively excluded from the analysis because they changed in occupancy status for *A. truei* between 2007 and 2008; *A. truei* was not detected in any of the three in 2007, but in all three in 2008 and both larvae and post-metamorphic animals were detected in two of the three basins in 2008, so reproductive occupancy was likely in at least two of these basins in 2007.

[58] Mean site index is scored as the average height of Douglas-fir at 50 years is an index of productivity and really reflects a combination of elevation, insolation and precipitation rates and soil type into an index value (Oliver and Larson 1996).

[59] The average size of non-fish-bearing basins has been demonstrated to increase dramatically with progressive inland position in Washington State (Palmquist 2005).

[60] This is especially true if one considers that occurrence is often patchy at small spatial scales. For example, see Diller and Wallace (1998). Moreover, Quinn and colleagues (2007) demonstrated that false negative errors did not decline substantially with light touch sampling methods until one exceeded 5 m of survey length (see their Table 4).

A relationship between lithology and landscape occupancy for *A. truei* seems less clear. Though Wilkins and Peterson (2000) found greater occupancy on basalt versus marine sedimentary lithologies (see also Dupuis *et al.* [2000]), Kroll and colleagues (2008) could not identify the same pattern over a broader area. Adams and Bury (2002) attributed this difference to a managed-unmanaged landscape dichotomy where lower occupancy on sedimentary lithologies in managed landscapes reflected forestry practices.[61] However, the study of Kroll and colleagues (2008), done solely on the managed landscape, does not support this hypothesis. These apparent differences between studies may simply reflect the greater breadth of sedimentary categories that Adams and Bury (2002) and Kroll and colleagues (2008) used in their studies, some of which may be unsuitable for *A. truei*. Nonetheless, ambiguity indicates that lithology-specific occupancy patterns still merit investigation. Further, the finding of Diller and Wallace (1999) that greater occupancy in younger managed stands probably reflects the relationship between the distribution of lithologies and historical patterns of harvest strongly underscores the need to consider landscape history when interpreting patterns.

RMZ-occupancy relationship that Stoddard and Hayes (2002) found indicated a need for some level of forested riparian margin, a result that should not be terribly surprising given that *A. truei* is restricted to forested landscapes. What is not clear from their work is whether a threshold forested width exists that results in a marked increase in occupancy or whether occupancy increases incrementally as the width of the forested riparian margin increases. As with some of the other patterns, the geographic generality of this notion is also unclear.

How general the influence of other landscape-level variables that have been shown to be significant in different studies is uncertain. For example, the significant increase in occupancy of post-metamorphic *A. truei* with elevation reported by Hunter (1998) may reflect a combination of the relatively limited elevation range that study encompassed and the seasonality in the habitat utilization patterns of adults in headwater streams (see Hayes *et al.* 2006).

Ascaphus montanus: Examining *A. montanus* distribution across the Flathead River drainage of northwestern Montana during the summers of 1966-1969, Franz and Lee (1970) found *A. montanus* present in a greater proportion of streams as elevation increased. In particular, they recorded it at 20% (n = 1) of five streams between 792–914 m (2,600–2,999 ft), 24% (n = 10) of 42 streams between 914–1,219 m (3,000–3,999 ft), 53% of 18 streams between 1,219–1,524 m (4,000–4,999 ft), 60% (n = 3) of five streams between 1,524–1,828 m (5,000–5,999 ft), and 67% (n = 2) of three streams between 1,828–1,920 m (6,000–6,300 ft). Notably, their data suggest that occupancy is over twice as high among streams at elevations $\geq$1,219 m (4,000 ft), although this increase with elevation would not be expected to be maintained into even higher elevation areas with heavy accumulations of ice and snow.

Based on work incidental to collecting data on sculpins[62] from 1967 to 1974, Maughan and colleagues (1980) summarized data on *A. montanus* distribution in north-central

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[61] Adams and Bury (2002) drew this conclusion based on the notion that sedimentary lithologies would show greater timber harvest-based sedimentation than basalt lithologies.

[62] Sculpins are primarily bottom-dwelling fishes (Roni 2002, 2003).

Idaho. Tailed frogs were recorded at 53 of 129 locations[63] in the Clearwater (n = 27), Coeur d'Alene (n = 9), Palouse (n = 8), St. Joe (n = 7), and St. Maries (n = 2) Rivers. Detectability of *A. montanus* using electrofishing units and kicknet sampling was not estimated, but Maughan and colleagues (1980) noted that Dean Metter had recently collected the species in at least three localities where electrofishing had not recorded it. Maughan and colleagues (1980) concluded that *A. montanus* was widespread, but appeared patchily distributed throughout headwater areas. They suggested that historic climatic conditions (glacial advance or retreat), sampling bias, or some other ecological factor associated with elevation could contribute to the observed pattern.

For tailed frog surveys conducted in the Wallowa Mountains of Baker, Grant, Umatilla, Union, and Wallowa Counties of northeastern Oregon in 1992-1993, Bull and Carter (1996a) subjectively selected 80 permanent, cold (< 20°C), small (< 5 m [16 ft] wide), high-elevation (> 1200 m [3.937 ft]) streams near (< 0.5 km) roads. Two surveyors searched each stream for 30 min by walking upstream over a 200-m (656-ft) reach and overturned rocks while a 16 cm × 15 cm (6.3 in × 5.9 in) dipnet was held immediately downstream of search locations. They recorded *A. montanus* at 53% of the streams (n = 42). The original set of streams was simply a screen to find *A. montanus*-occupied streams for more intensive study, so data on habitat differences between occupied and unoccupied streams was not obtained.

In the southeastern Kootenay region (British Columbia), Dupuis and colleagues (2000; see also Dupuis and Wilson 1999) sampled 188 streams in 1996 and 1998 over a 2,000-km^2 (772-mi^2) area encompassing the one previously confirmed tailed frog record using the selection of permanent streams and TCS sampling approaches previously described for their work on *A. truei* (see page 19). However, these surveys differed in that the landscape was entirely road-accessible, and they sampled all permanent streams within the 2,000-km^2 (772-mi^2) footprint. *Ascaphus montanus* were found in 17 (9%) streams. The exploratory sampling pattern likely contributed to a low occupancy rate since it included areas both elevationally and geographically outside of the occupied range as it is now understood, but low detectability associated with applying a 20-min TCS survey approach may have also contributed to underestimating occupancy (see page 19). The primary objective of this effort was to gain an idea of the regional footprint over which tailed frogs might occur.

In a more comprehensive effort across the range of *A. montanus* in Canada, Dupuis and Friele (2006) conducted 30-min TCS surveys at 236 locations; 156 were in the Flathead drainage, the other 80 were in the Yahk drainage. They found *A. montanus* at 39% (n = 61) of Flathead locations and at 80% (n = 64) of Yahk locations. They concluded that *A. montanus* is limited in distribution to basin sizes ranging from about 0.3 to 100 km^2 (0.1 to 39 mi^2), but occupancy based on larvae seemed greatest at basin sizes of 0.5-35 km^2 (0.2-14 mi^2). This pattern led them to hypothesize that the relationship between tailed frog distribution and basin area reflects changes in channel process domain and regional stream discharge over the gradient in basin sizes. In particular, they postulated that tailed frogs are adapted to cascade and step-pool channel morphologies of these small basins, presumably because they afford greater bedform stability and pore-space refugia than either the smaller colluvial headwaters or floodplain plane bed and pool-

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[63] Based on Maughan (1972), sampling locations were approximately 16 km (9.9 mi) apart.

riffle bedforms of larger streams. The large difference in occupancy between the Yahk and Flathead drainages largely reflected the fact that the warmer wetter biogeoclimatic zones, in which *A. montanus* were detected much more frequently, were all in the Yahk watershed (Dupuis and Friele 2006). Based on a Principle Components Analysis, they found that the landscape variables basin size, relief,[64] elevation, and biogeoclimatic zone explained slightly over 50% of the variation in *A. montanus* occupancy patterns.

In a retrospective study of stream temperatures related to disturbance history, Dunham and colleagues (2007) selected 30 reaches in each of three major disturbance categories across nine streams in the Boise River Basin in central Idaho.[65] In the summer of 2003, each 100-m (328-ft) reach[66] was electrofished using a four-pass removal method for sampling fish and amphibians.[67] The focus was the two regionally most common native species, *A. montanus* and rainbow trout (*Oncorhynchus mykiss*). Validation done in 2002 revealed that this level of effort was nearly 100% effective in detecting salmonid fishes (Rosenberger and Dunham 2005); detectability via electrofishing was unknown for adult or larval *A. montanus*. Nonetheless, the striking feature of this study was the high level of occupancy exhibited by *A. montanus*, despite the fact that selection was random within the landscape sampling frame of headwater streams draining catchments 1,000-5,300 ha (3.9-20.5 mi^2) in size.[68] In particular, *A. montanus* larvae were detected in 94% (n = 85) of streams. Further, the species showed no differences in occupancy among streams in the three disturbance categories.[69]

In summary, landscape-level data for *A, montanus* are sparser than for *A. truei*, limiting conclusions. However, the finding of Dupuis and Friele (2006) that occupancy appears greatest in basins of relatively small sizes echoes the quadratic relationship with basin size Hunter (1998) and Kroll and colleagues (2008) reported for *A. truei*. Further, the apparent mid-elevation lower limit of *A. montanus* distribution first commented on by Franz and Lee (1970) and alluded to by Maughan and colleagues (1980) and Dupuis and Friele (2006) may simply reflect the condition that suitable habitat over the area of *A. montanus* range is absent at lower elevations.

Considering both species, tailed frogs appear irregularly distributed across landscapes, though clearly this statement must be caveated by the scale and effort addressed. The few studies with high levels of occupancy at the level of different streams or reaches within streams (e.g., Dupuis and Friele 2006, Dunham *et al.* 2007, Kroll *et al.* 2008) had more intensive sampling regimes, which suggests that incomplete detection may have been an issue in previous studies. Thus, characterizing landscape occupancy patterns that avoid

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[64] Dupuis and Friele (2006) defined relief as the height in meters in the drainage above the sample point.

[65] The three categories were: 1) streams without recent stand-replacing wildlife in their watersheds; 2) streams with a recent history of moderate to high severity wildfires predominant in their watershed; and 3) streams in watersheds with a history of moderate-high severity wildfire that were followed by massive channel reorganization from a debris flow or a severe flood (Dunham et al 2007). Wildfires in stream catchments selected for comparison occurred in 1992 and 1994, with channel reorganizing events occurring immediately after wildlfires in the “burned and reorganized” stream category followed by subsequent recurrences of varying magnitude 1-2 years post-fire.

[66] Sampled reaches were block net-delimited.

[67] All sampling was done during base flow conditions from mid-July to mid-September. The sampling schedule was rotated among streams in each disturbance category to avoid any potential confounding of stream type and time of sampling.

[68] Selection of these relatively small catchment sizes was to increase the likelihood that a disturbance-related effect might be detected (Dunham *et al*. 2007).

[69] *Ascaphus montanus* larvae were not detected at two sites in each of the unburned, and burned and reorganized categories; and at one site in the burned category (see footnote 65 for category details).

underestimation requires careful attention to sampling approach and level of effort.

In both species, basin size was related to occupancy (Hunter 1998, Dupuis *et al*. 2006, Hayes *et al.* 2006, Kroll *et al.* 2008). Dupuis and Friele (2006) initially suggested the conceptual mechanistic model for this relationship, the gradient in channel processes and stream discharge. This model makes sense for the upper limits of instream distribution and is consistent with physical characterizations derived from these processes (Brummer and Montgomery 2003), but it competes, and not necessarily mutually exclusively, with potential biotic factors (e.g., competition with or predation by fishes or crayfishes) for explaining the downstream limits of distribution (Creed 2006, Hayes *et al*. 2006, Kroll *et al*. 2008).

Other factors, such as lithology (Wilkins and Peterson 2000), may also influence tailed frog distribution. Categorization of lithologies and the diverse mosaic of those lithology types in landscapes may limit our ability to interpret precisely how lithology influences their distribution. This may be the basis of the studies of Adams and Bury (2002) and Kroll and colleagues (2008) being inconsistent with the finding of Wilkins and Peterson (2000). Further, Sutherland (2000) speculated that disturbance history within drainages may also influence tailed frog occurrence, but disturbance type and magnitude is likely important. For example, fire and channel reorganization disturbance in one study of *A. montanus* did not appear to influence occurrence, at least over the short (few-year) time scale examined (Dunham *et al*. 2007) and the Mt. St. Helens eruption seems to have had limited impact on genetic structure (Spear *et al*. 2012). As Kroll and colleagues (2008) emphasized, understanding the factors that appear to limit tailed frog distributions is only now beginning to be realized.

Landscape-Level Abundance: Patterns of tailed frog abundance across landscapes are even more difficult to infer than landscape patterns in occupancy for the same reasons (see *Landscape-Level Occupancy* section introduction). The greater number of variables potentially affecting abundance and their interactions no doubt contribute to this pattern.

Ascaphus truei: Besides his analyses of occupancy, Welsh (1990) reported a significant relationship between an abundance surrogate (captures/m^2) and forest age, though this relationship was significant only for his low-elevation sites (<1000 m [3,281 ft]) and had limited explanatory power ($r^2 = 0.285$).[70] Welsh (1990) also reported a significant negative relationship between these abundance data and stream temperature, but in this case, he included all sites. He described stream temperature as an excellent predictor of abundance though its explanatory power ($r^2 = 0.373$)[71] was only slightly better than that of the abundance–forest age relationship. Welsh (1990) argued that lack of a strong relationship between tailed frog abundance and forest age reflected the fact that age was an indirect measure of the macro- and microhabitat elements limiting tailed frog distribution. Assuming the unexplained sampling frame and small sample sizes in his

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[70] Welsh (1990) had 26 sites in his low-elevation category. He described the relationship between *A. truei* relative abundance and forest age using an unreported linear regression, but the equation is Relative Abundance = 0.677 + 0.000475*Forest Age (H. Welsh, 2014, pers. comm.). Relative abundance was based on the square root transform of captures/m^2. The 95% confidence interval around the slope (upper CI = 0.0010; lower CI = 0.0002) excluded zero.

[71] Welsh (1990) also described the relationship between *A. truei* relative abundance and temperature based on a simple linear regression, which he did not report, but the equation describing the relationship was relative abundance = 1.909 - 0.078*temperature. The 95% confidence interval around the slope (upper 95% CI = -0.046; lower 95% CI = 0.111) did not encompass zero.

younger forest age categories did not compromise his interpretation of the study (see page 17), Welsh (1990) described modest relationships between each of forest age and abundance at low elevations, and stream temperature and abundance. However, his coefficients of determination reveal that in both relationships, most variability was not explained.

In their characterization of the terrestrial amphibian assemblage in the Oregon Coast Range (see page 17), Corn and Bury (1991) also provided selected data on landscape-level abundance[72] for *A. truei*. In particular, they observed no difference in abundance for post-metamorphic *A. truei* pitfall-trapped among their young, mature, and old-growth stands (see footnote 28). The average number trapped per 100 trap nights in mature stands (0.101) was three times that in either old-growth (0.033) or young (0.035), but variability among stands was high. A substantial portion of that variability may reflect proximity of perennial streams to individual stands (see page 18). However, Corn and Bury did find that the mean abundance of pitfall-trapped post-metamorphic *A. truei* was significantly greater in the five wet old-growth stands (0.153/100 trap nights) than in the 14 old-growth stands with moderate moisture levels (0.032/100 trap nights; $F_{2,24} = 10$; $P = 0.001$). The latter agrees with the high moisture requirements of *A. truei* (see LIFE HISTORY section), but lability of pitfall sampling to seasonal variation (Bury and Corn 1987) makes describing abundance patterns using this method risky.[73]

In a companion study, Gilbert and Allwine (1991) examined the terrestrial amphibian assemblage in the Oregon Cascades using pitfall trapping, but also conducted time-constrained searches.[74] Pitfall trapping was done in September and October 1984 using grids similar to those Corn and Bury (1991). Sampling was done in each of 56 stands in three areas (stand numbers in each area in parens): near Mt. Hood in the northern Oregon Cascades (16), on the H.J. Andrews Forest in the central Oregon Cascades (20), and in the Rogue-Umpqua area of the southern Oregon Cascades (20). As in the Corn and Bury (1991) study, stands were classified into young, mature, and old-growth, but stand age category groupings differed slightly.[75] Pitfall trapped post-metamorphic *A. truei* suggested an abundance gradient that increased from south to north,[76] reflecting a latitudinal moisture gradient. Further, the differential association of post-metamorphic *A. truei* with stands of different ages seems to reinforce the gradient idea; *A. truei* was associated with young stands near Mt. Hood, with mature stands on the H.J. Andrews, and only with old-growth in Rogue-Umpqua stands.

In a second companion study, Aubry and Hall (1991) studied the terrestrial amphibian assemblage in the Washington Cascades using the same pitfall trapping array approach.

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[72] Expressed as the number of individuals captured per 100 trap nights of pitfall trapping (see page 17 for details).

[73] Where sampling is done with replacement (not in the case of Corn and Bury [1991]), pitfall trapping would only index abundance, which would complicate interpretation.

[74] Time-constrained searches consisted of searching each stand intensively for four person-hours. However, time-constrained searches, which occurred in the spring of 1984, yielded too few captures of post-metamorphic *A. truei* (specifically only two) so will not be considered further here.

[75] Young stands were 30-80 years, mature stands were 80-200 years, and old-growth were >200 years (Gilbert and Allwine 1991).

[76] This was based on an ANOVA specified as significant at $P < 0.05$; mean abundance values (number of captures/ number of trap grids) across the three areas were: 0.2 (Rogue-Umpqua, 1.9 (H.J. Andrews), and 12.3 (Mt. Hood). Uncertainty about these abundance values is based in part on the comment that animals were either released at the capture location or preserved for food habit studies without specified of either what proportion of animals were preserved or how much of this applied to *A. truei*.

Pitfall trap sampling was done without replacement after the onset of fall rains in 1984 and 1985[77] in stands across age and moisture gradients.[78] Aubry and Hall (1991) found significant differences among stand age groupings for post-metamorphic *A. truei*. In particular, *A. truei* were more abundant in mature stands than in young stands, but they showed no particular association with old-growth. Moreover, unlike Corn and Bury (1991), Aubry and Hall (1991) found no significant differences in *A. truei* abundance among stands with different moisture levels.[79] Aubry and Hall (1991) also found that *A. truei* displayed a positive relationship to elevation and gradient and were associated with the presence of water.

Also in western Washington, Kelsey (1995) sampled 28 streams in 1992 and 1993 in 40-to-60-year-old stands harvested previously once, and which represented the pre-harvest years for two related manipulative studies (Kelsey 1995, 2000).[80] Surveys for stream-breeding amphibians, including *A. truei*, were conducted within a 300-400-m basal target segment within which two or three 10-m long survey units were randomly selected for block net sampling.[81] Unfortunately, post-hoc biogeographic evaluation revealed that five of the 28 streams came from an area where *A. truei* has been shown to be largely absent, the Black Hills; this species is restricted to only a few streams along their northern margin (Kelsey 2000). Excluding those five sites, densities of *A. truei* averaged 0.83/m^2 ± 1.53 (range: 0.00-6.73/m^2).[82] However, as only 10 of these sites had been selected based on presence of any stream-associated amphibians (see footnote 80), sampling during the entire period that involved these manipulative studies (four years over a five-year span [1992-1993, 1995-1996]; Kelsey 1995, 2000) revealed that *A. truei* was also never recorded at six more of these 23 sites, one of which was an unharvested control. Hence, if one considers *A. truei* densities across the 17 managed sites over the 1992-1993 pre-treatment period where *A. truei* was known to present

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[77] To prevent bias from the depletion of individuals in the immediate area of sampling in 1984, Aubry and Hall (1991) moved each grid about 50 m within the stand in 1985.

[78] The age gradient consisted of nine young, nine mature, and 19 old-growth stands, whereas the moisture gradient consisted of seven dry, 12 moderate, and nine wet stands, all of which were old-growth. All 19 old-growth stands in the age gradient were also in the moisture gradient (Aubry and Hall 1991). Age distributions of young stands were 55-75 years, mature stands were 90-190 years, and old-growth was 210-730 years. Because samples from 1984 and 1985 were not independent, Aubry and Hall (1991) use the mean value of captures for *A. truei* from both years in all analyses. They calculated abundance indices for amphibian species as captures per 100 trap-nights for each stand.

[79] The mean abundance index values for stands classed as dry were lower than those classed as moderate or wet, which were similar; but the variation in the abundance index among stand moisture classes was high.

[80] Study streams were located in the western Washington Cascades between Interstate 90 and the Columbia River (Kelsey 1995). Ten streams were selected based on the presence of at least one species of stream-breeding amphibian had been verified prior to sampling; the remaining 13 streams were selected without prior knowledge of stream-breeding amphibian occupancy. Ten of the 23 streams were also fish-bearing (containing at least one salmonid or cottid fish species), but which fish-bearing streams were also ones when presence of at least one stream-breeding amphibian species was known was not indicated.

[81] Basal target segments were 300 m in 10 streams and 400 m in the remaining 18 streams. Moreover, six of the 28 sites were surveyed twice in 1993; all other sites were surveyed three times in either 1992 or 1993. The block net sampling approach used involved placing 3.125 mm-wire screening at each of the downstream end and the 3.5- and 7-m points of each randomly chosen 10-m survey unit within the aforementioned 300- or 400-m basal target segments. Within each 10-m survey unit, all rocks and logs were removed beginning at the downstream end and working upstream. Aquarium nets and screening was used to capture all amphibians observed. These were held for processing (measuring and weighing). After completing the initial survey prior to releasing animals, the 10-m survey unit was checked for any amphibians that might still be present. After this check and their processing, all rocks and logs were returned to the channel in a pattern resembling their original configuration, animals were released, and the block net screening removed.

[82] Unit of variation is the standard deviation.

(that is, recorded in at least one year during these studies), *A. truei* densities averaged 1.12/m^2 ± 1.7 (range: 0.02-6.73/m^2). Selected features of stream sites were measured, but no stream site features could be clearly associated with variation in larval *A. truei* densities.

One focus of Adams and Bury (2002) study on the Olympic Peninsula was examination of relative abundance patterns for *A*, *truei*. This analysis used a 141-stream subset of the 163 streams surveyed (M. Adams, 2014, pers. comm.). Density (captures/m^2) was the relative abundance measure. Three landscape variables (elevation, gradient, and aspect)[83] had significant relationships to density. *Ascaphus truei* density increased with elevation but declined as aspect moved further from north. The relationship to gradient was more complex as analysis suggested density peaks at both moderate (20-25%) and steep (>50%) gradients (Figure 2 in Adams and Bury 2002). Whether the latter is an artifact of either the few high density-steep slope points or lack of much landscape at intermediate gradients or reflects some actual asymmetry, such as differential use of gradients by life stage, is unclear.[84]

In summary, landscape patterns related to abundance in *A. truei* are complicated to infer because studies attempting to estimate abundance have often been regionally restricted, making geographic inference difficult; sampling methods may be vulnerable to seasonal vagaries (pitfall trapping), resulting in abundance indices that are difficult to interpret; or the sampling method assumes perfect detectability or detectability proportional to abundance, resulting in abundance estimates that are potentially biased in unknown ways. Nonetheless, the Gilbert and Allwine (1991) study suggests that the latitudinal gradient in moisture along the Oregon Cascades may strongly influence abundance and may be intrinsically tied to habitat use patterns in *A. truei*. The finding of Aubry and Hall (1991) that *A. truei* does not appear to associate with old-growth in Washington State suggests that such a gradient extends north.

Ascaphus montanus: Dupuis and Friele (2006) drew similar conclusions regarding *A. montanus* density that they did for occupancy (see page 25) with caveats. Larval *A. montanus* appeared most abundant at basin sizes ranging from 1 to 20 km^2 (0.4 to 7.7 mi^2), though they were recorded in basins ranging in size from 0.5 km^2 (0.2 mi^2) to just over 100 km^2 (39 mi^2). In contrast, post-metamorphic *A. montanus* seemed down-shifted in basin sizes, being most abundant at basin sizes ranging from 0.3 to 17 km^2 (0.1 to 6.6 mi^2), though they were recorded in basins ranging in size from 0.2 km^2 (0.08 mi^2) to just over 100 km^2 (39 mi^2). A down-shift in basin size is equivalent to an up-shift in elevation all else being equal, so this pattern is similar to the within-stream elevation differential between larvae and post-metamorphs reported for *A. truei* (Hunter 1998, Hayes *et al.* 2006).

In their retrospective stream temperature-disturbance history study across 90 sites, Dunham and colleagues (2007) found no obvious relationship between the numbers of *A. montanus* larvae using their four-pass electrofish sampling and stream temperature. However, this pattern was not part of their formal analysis as individual detectability information for *A. montanus* larvae was unavailable.

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[83] Elevation was obtained from 1:62500 USGS topographic maps. Gradient was averaged from three points measured at the 25, 50, and 75 m locations in each 100 m reach sampled. Aspect was measured to the nearest degree as the deviation from north.

[84] Density data included life stages collectively.

In summary, landscape patterns for *A. montanus* abundance may be no less complicated than those for *A. truei*, and we expect that inference on patterns is generally constrained by the same conditions. Variation in abundance with the basin size that Dupuis and Friele (2006) reported in *A. montanus* may have a parallel in *A. truei* since the basin size relationship to occupancy appears similar in both species. However, whether the apparent latitudinal moisture gradient in *A. truei* can be expected for *A. montanus* is unclear because *A. montanus* has a far more restricted latitudinal range and whether the more variable interior climate that influences *A. montanus* varies enough over its range to influence a cline in abundance is unclear.

Genetic Patterns and Distribution: Genetic data has provided insights into connectivity among tailed frog populations at geographic and smaller landscape scales.

Ascaphus truei: Beyond identifying genetic groups concordant with what would later become the two tailed frog species currently recognized, Daugherty (1979) identified significant genetic structure within *A. truei*. His examination of allele frequencies at 23 allozyme loci in 5 to 61 individuals from 20 sites (634 individuals overall; see Nielson *et al.* 2006) showed some differentiation among *A. truei* from the Cascade Mountains, the Coast Ranges of Oregon, the Klamath-Siskiyou Mountains of California, and Olympic region of Washington.

Using a 169-loci RAPD analysis (see footnote 18), Ritland and colleagues (2000) revealed strong groupings of *A. truei* in mid/north-coastal and south coastal British Columbia. Within these regions, genetic distance appeared unrelated to physical distance and estimates of population differentiation were moderately low (F_{ST} = 0.02-0.05)[85]. Further, gene diversity in south-coastal populations was estimated to be about 25% less than that in mid/north-coastal populations. Ritland and colleagues (2000) interpreted these data to reflect historic restriction of *A. truei* in British Columbia into at least two refugia from which subsequent re-expansion occurred.

In their tailed frog phylogeography, Nielson and colleagues (2001) sampled 24 larvae from 9 populations over *A. truei* range in Oregon and Washington. Using sequences from mitochondrial cytochrome and NADH genes to examine genetic structure, their analysis supported the findings of Daugherty (1979), revealing differentiation among the Olympic Mountains, North Cascade Mountains (Washington), Coast Ranges and Siskiyou Mountains (Oregon).

Spear and Storfer (2008) contrasted *A. truei* at 20 sites across unmanaged forest areas in Olympic National Park (ONP) with 18 sites on the Olympic National Forest (ONF) located in a landscape with varying amounts of timber harvest. Sample sizes, described as sufficient at each site, had only the means reported for the two site groups.[86] All loci and populations were in Hardy–Weinberg equilibrium except for one locus at one site each on the ONP and ONF, and only two pairs of loci (out of 78 comparisons) were out of linkage equilibrium, a pattern not different from random. Both genetic diversity and gene flow were high among sites in each region. The number of alleles ($\bar{x}$ = 21 alleles/locus in ONP; $\bar{x}$ = 25 alleles/locus in ONF) and heterozygosity (0.855 in ONP; 0.912 in ONF) were high. Based on F_{ST} values, little population subdivision appeared

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[85] F_{ST} or Fixation index is a measure of population differentiation based on genetic polymorphism data, such as single nucleotide polymorphisms (SNPs) or microsatellites (Hudson *et al*. 1992).

[86] Sample sizes at ONP averaged 26, whereas sample sizes at ONF sites averaged 28.

apparent (ONP F_{ST} = 0.03; ONF F_{ST} = 0.004). Standardizing these values using G'_{ST}[87] yielded 0.16 (95% CI: 0.11–0.22) for ONP and 0.04 (95% CI: 0.03–0.05) for ONF. Therefore, genetic differentiation appeared higher (and connectivity lower) across ONP relative to the ONF. However, Spear and Storfer (2008) interpreted less differentiation across the managed landscape to reflect a historical signature of continuous forest before harvest began. Two important considerations weaken this inference; sites were not randomly chosen on the unmanaged forest study area and the authors did not effectively exclude the alternative that less differentiation simply reflects exchange that is more panmictic in the lower elevation ONF than the generally higher elevation ONP.

In summary, save the study of Spear and Storfer (2008), collective genetic analyses to date have characterized seven units within *A. truei* that correspond reasonably well to geographic areas: mid/north-coastal and south-coastal British Columbia, the Cascades of Washington and Oregon, the Olympic region of Washington, the Coast Ranges of Oregon, and the Klamath Siskiyou region of Oregon and northern California. In the Olympic region, Spear and Storfer's (2008) hypothesis that less genetic differentiation and greater connectivity in the Olympic National Forest than in Olympic National Park reflects a historical signature of continuous forest needs testing to determine whether a trajectory toward greater differentiation is actually occurring.

Ascaphus montanus: Daugherty (1979) also identified significant genetic structure within what would ultimately become *A. montanus* range. He examined allele frequencies at 23 loci in 5 to 60 individuals from 14 sites (471 individuals overall) across *A. montanus* range (see Nielson *et al.* 2006). As with *A. truei*, he found population clustering at the scale of mountain ranges, that is, *A. montanus* from two different ranges in the Rocky Mountain axis and the Blue-Wallowa complex of southeast Washington and northeast Oregon appeared differentiated.

The RAPD analysis of Ritland and colleagues (2000) revealed high estimates of differentiation (F_{ST} = 0.18) within the interior population cluster, the population systems in British Columbia ultimately attributable to *A. montanus* (Adams and Pearl 2005b). Moreover, a strong relationship existed between genetic distance and physical distance in this population cluster. Ritland and colleagues (2000) interpreted these data to reflect relatively limited gene flow among populations within this cluster.

Nielson and colleagues (2001) sampled 56 larvae from 14 populations over the range of *A. montanus* in Washington, Idaho, and Montana. Using the mitochondrial gene sequences noted previously, their analysis revealed differentiation between the Rocky and Salmon River Mountains and thus reinforced some findings of Daugherty (1979) about *A. montanus*.

In follow-up to their earlier work, Nielson and colleagues (2006) sampled an additional 60 larvae from 12 populations over the range of *A. montanus* that did not overlap with their previously sampled populations. Again using mitochondrial genes, their analysis reinforced the pattern of the two populations clusters revealed in earlier work: one comprising the populations south of the South Fork of the Salmon River (Salmon River Mountains, Idaho) and other comprising all other *A. montanus* populations analyzed.

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[87] G'_{ST} is a standardized measure of genetic distance based on the Weir and Cockerham (1984) adjustment of F_{ST} that divides the estimated F_{ST} by its upper limit [the value if two populations share no alleles]. This is useful with high allelic diversity and an F_{ST} upper bound of < 1, frequent with microsatellites.

They regarded these clusters as ESUs notwithstanding the fact that clustering based on their allozyme analysis (based on Daugherty 1979) was discordant and that almost all population pairs across *A. montanus* geographic range show significant F_{ST} values.

In a landscape study conducted across north-central Idaho, Spear and Storfer (2010) sampled 41 sites across a 13,000 km^2 (5,019 mi^2) area. They divided the area into two regions based on land use. A 4,500 km^2 (1,737 mi^2) northern region consisted of forest managed by several landowners and used primarily for timber harvest,[88] and an 85,000 km^2 (1,737 mi^2) southern region that occurs almost completely within the Clearwater National Forest and contain largely roadless areas separated by only thin boundaries of roads.[89] Potential sampling sites within the northern region were based on a stratified random sample having either high or low canopy cover,[90] whereas potential sampling of sites in the southern region were based on roadless area presence or absence. Within these strata, actual sites used were determined by accessibility and abundance of tailed frogs. Based on 1,009 *A. montanus* sampled across the 41 sites,[91] Spear and Storfer (2010) used a suite of landscape genetic techniques[92] to compare alternative paths of connectivity[93] among sites across burned and harvested forests. They then determined the values of independent variables[94] along each path route and tested the relationship

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[88] Potlatch Corporation, the Idaho Panhandle National Forest, and Idaho Department of Lands were primary.

[89] The southern region had a reduced history of timber harvest, but much of the area had been influenced by fire, especially as the result of the Great Burn fire of 1910, which burned much of central Idaho and western Montana over the course of two days (Spear and Storfer 2010). Very large fires also occurred in 1919 and 1934, and the region has a regular history of smaller fires continuing until the present. Hence, most of the disturbance in this area occurred before extensive human incursion.

[90] Defined as ≥50% and <50%, respectively.

[91] Each site was represented by no fewer than 20 and no more than 30 individuals.

[92] Spear and Storfer (2010) determined whether loci and sites were in Hardy-Weinberg equilibrium and linkage equilibrium. For each site, they also calculated allelic richness, the inbreeding coefficient (F_{IS}), and observed and expected heterozygosity. All four metrics provide insight into the amount of genetic diversity in a population. Allelic richness and heterozygosity are positively related to increasing genetic diversity. Increasing positive values of F_{IS} indicate non-random mating of closely related individuals that may lead to decreased genetic diversity. Further, they estimated among-site differentiation using G'_{ST}, which estimates differentiation based on heterozygosity and assumes equilibrium, and the proportion of shared alleles (D_{ps}), which is based on allele frequencies and not subject to equilibrium assumptions. Each of these two measures increases in value with increasing genetic differences among populations, and thus, both are negatively correlated with gene flow. Spear and Storfer (2010) also tested whether populations had experience population size declines via three methods: tests for heterozygosity excess, shifted allele distributions, and estimation of M-ratios. They used all three tests because of the different time scales associated with each method.

[93] Spear and Storfer (2010) used a least-cost path methodology to test the hypothesize influence of landscape and climatic variables in the northern and southern study regions. They developed seven different paths of connectivity among sites, including paths based on straight-line distance, fire history, canopy cover, heat-load index, and stream distance. The first path was simply a straight line connecting all sites, a path that could be expected if no landscape influence existed on gene flow as assumed under a simple distance by isolation model; this path was the reference or control alternative. Next they created two paths based on fire history. Both regions compared had fires from the year 1900 to present, however, as fire occurrence is a categorical variable, a cost value had to be assigned to burned areas and data to guide cost assignment was lacking. Hence, two alternative cost ratios were examined (2:1 and 10:1) in which unburned areas were given a cost of 1 and burned areas were given the higher cost. The fourth path was the least cost path maximizing movement through canopy cover. This path serves as proxy for timber harvest as Spear and Storfer (2010) lacked specific harvest data for the entire region. The fifth path was one minimizing the heat load index. In addition, because interaction between canopy cover and solar radiation (as measured by the heat load index) was suspected, they created a sixth least-cost path by combining these two variables. The final least-cost path maximized movement along stream corridors.

[94] To incorporate fire history, Spear and Storfer (2010) calculated the total distance that the route traveled through burned areas. Remaining variables were all continuous, so they calculated a weighted average along each path for each variable. Those variables included canopy cover, the heat load index, the number of frost-free days, and the growing season precipitation.

between the variables along each route with the two measures of genetic differentiation using geographically weighed regression (GWR) analysis.[95] GWR analyses revealed that both forest canopy cover and stream distance were correlated with genetic distance across the harvested region, which implies that gene flow among sites in the harvested region occurs along multiple corridors, and hence, is less appropriate for a single path approach. For this reason, Spear and Storfer (2010) used circuit theory algorithms[96] to model gene flow across the harvested subregion using. Circuit theory allows for multiple pathways for gene flow, providing an appropriate modeling framework if individuals are following both forested and riparian corridors.

Spear and Storfer (2010) found no evidence of differences in measures of genetic diversity between the two areas. In particular, genetic diversity was high across both areas based on both allelic richness (harvested = 10; roadless = 10.12) and expected heterozygosity (harvested = 0.840; roadless = 0.819). Moreover, though significantly high F_{IS} values (see footnote 92) existed at some sites, the harvested area had a mean F_{IS} of 0.08 and the roadless area had a mean F_{IS} of 0.07. However, the global G'_{ST} for the harvested area was 0.054 (95% confidence intervals [CI] = 0.022-0.099), whereas that for the roadless areas was 0.024 (CI = 0.012-0.042). Though overlap exists in the 95% confidence interval, Spear and Storfer (2010) interpreted these data to mean that greater genetic differentiation existed in the harvested area, but the reduction in gene flow had not yet resulted in a reduction in genetic diversity. Spear and Storfer (2010) also found no evidence of recent population size declines.[97]

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[95] Geographic weighed regression (GWR) analysis is a modification of spatial regression analysis that accounts for local differences (Fotheringham et al. 2002). It is similar to global spatial autoregression analysis in that a spatial weighing matrix (a matrix of values that describe the spatial relationship among points) is used to incorporate a spatial component into the regression equation. However, GWR is performed by estimating regression parameters at each data point using only data points within a specific bandwidth of the focal point and including a spatial weight in the local equation. To create a spatial weighing matrix based on distance requires that the matrix be based on point values. However, Spear and Storfer's (2010) differentiation measures were based on lines that connect site pairs, so they designated the mid-point of the straight-line route as the basis for the spatial weighing matrix. To produce a weight from these midpoints, Spear and Storfer (2010) used a bi-square weighing function in which the spatial weight between two sites i and j is calculated as $w_{ij} = \left(1 - \left(d_{ij}/b\right)^2\right)$, where d represents the distance between the two midpoints and b is the bandwidth. The best GWR model across all potential paths was chosen based on Akaike Information Criterion (AIC) weights. The final step was to examine whether local variation existed across each subregion with respect to how much variation was explained by the best overall model at each data point. To do this, Spear and Storfer (2010) calculated the Getis-Ord statistic using the adjusted $r^2$of each local regression. The Getis-Ord statistic is a measure of whether high and low values of a variable are clustered (Getis and Ord 1995). The Getis-Ord statistic is a Z score, so a score >1.96 indicates significant clustering of high values (hot spots) and a score <-1.96 indicates significant clustering of low values (cold spots). In the case of Spear and Storfer (2010), hot spots were areas that fit the model especially well.

[96] Spear and Storfer (2010) used CIRCUITSCAPE software (McRae and Shah 2009) to do this analysis. CIRCUITSCAPE requires the input of a single cost surface and sampling points and calculates a single value representing the total for each pairwise comparison. Spear and Storfer (2010) input three resistance surfaces. Two of these were identical to the cost surfaces used in the least-cost analysis: canopy cover and stream distance. Spear and Storfer (2010) also calculated an added cost surface that combined canopy cover and stream distance. This surface was a canopy layer modified so that all stream pixels had a cost of 1 regardless of canopy cover. This third surface enable Spear and Storfer (2010) to test their post-hoc hypothesis that populations are simultaneously using both riparian and forested paths.

[97] Lack of evidence of populations declines was based on no significant excesses in heterozygosity, no shifted allele frequencies, and no significantly low M-ratios when compared to the M_C ratios for each site. The M-ratio is the ratio of the number of alleles (k) to the allelic size range (r), which can represent a signature of more historic decline as not every new allele in a recovering population will increase k relative to r. It is possible to calculate a critical M-ratio (M_C), with values lower than the critical number indicating declines.

Across the harvested area, Spear and Storfer (2010) found that the best supported model followed the riparian least-cost path and included total topographic distance (positively correlated with G'_{ST}) and growing season precipitation (negatively correlated with G'_{ST}). In the roadless area, the best supported model minimized movement through areas with high solar radiation and included topographic distance through burned areas (positively correlated) and heat load index (negatively correlated). Further, results of the hot/cold spot analyses (footnote 95) from the local regressions of the overall best model across the harvested area identified two hot spots and one cold spot. Hot spots coincided roughly with private timberlands, whereas the cold spot stretched across primarily publicly owned land. In the roadless area, hot/cold spot analyses revealed a north-south divide; the largely unburned north subarea was a cold spot and the largely burned south subarea a hot spot.[98]

In conclusion, the genetic data of Spear and Storfer (2010) appear to indicate that the response of *A. montanus* fire differs from its response to timber harvest. Higher genetic connectivity across the fire-dominated roadless area is consistent with the idea that fire limits gene flow less than harvest; nonetheless, alternative reasons for greater genetic connectivity in the roadless area have not been effectively excluded. The difference in connectivity could not be attributed to isolation by distance because the harvested area is only slightly over half the size of the roadless area. Further, as Spear and Storfer (2010) note, patterns of genetic connectivity are even more surprising when contrasted to their study of *A. truei*, the sister species of *A. montanus*, on the Olympic Peninsula because genetic connectivity patterns in *A. montanus* appear to be greater than those of *A. truei* despite *A. montanus* inhabiting the more xeric landscape. Precipitation was a pivotal variable explaining genetic variation in *A. montanus* across the harvested area (Spear and Storfer 2010), but precipitation did not appear important to any of the *A. truei* models explaining genetic variation on the Olympic Peninsula (Spear and Storfer 2008). This suggestion of precipitation limitation and that fact that the best model had strong support for least-cost movement along stream paths led Spear and Storfer (2010) to conclude that *A. montanus* used riparian corridors to actively avoid the disturbed areas during harvest. However, this contention needs further examination because Spear and Storfer (2010) also found empirical support for movement along least-cost canopy paths; their harvested and roadless areas was, at best, geographic partitioning that is data noisy; an understanding of movement patterns in post-metamorphic *A. truei* is almost entirely lacking; and greater genetic connectivity that *A. montanus* seems to display relative to *A. truei* may conceal unique movement dynamics in the former.

In summary, excluding the study of Spear and Storfer (2010), collective genetic studies of *A. montanus* reveal significant genetic partitioning across three geographic areas: the Rocky, Salmon River, and Blue-Wallowas Mountains. Though genetic analysis of *A. montanus* between Canada and the United States have never been combined, it is presumed that the disjunct Canadian populations that Ritland and colleagues (2000) studied are northern extensions of the first two of the above areas. Lastly, contrasting the work of Spear and Storfer (2008) on *A. truei* with their work on *A. montanus* (Spear and Storfer 2010) revealed unanticipated genetic asymmetries that may have roots in fundamental biological differences between the two species that need exploration.

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[98] No puns intended.

STATUS

Glenn Sutherland, Linda Dupuis, Marc Hayes, and Tanya Wahbe

Management and conservation concern for each of the tailed frog species varies among political entities across their respective geographic ranges (Table 1). Reasons for this also vary, but include: 1) a limited geographic range; 2) demographic characteristics thought to make each species vulnerable (namely a long [often multi-year] larval interval, and low fecundity and high site fidelity in adults); and 3) habitat requirements for small, permanent, forested streams with water quality characteristics (usually described as clear [non-turbid] and cool [low temperature]) that are thought to make their habitat vulnerable to disturbance. The empirical basis of the vulnerability of tailed frogs and their habitat is a focus of this review; this section describes the designations reflecting current levels of concern for each species across their ranges.

TABLE 1. *Ascaphus truei* status across its geographic range (November 2014).

COUNTRY	PROVINCE/ STATE	STATUS	SOURCE
Canada	—	Special Concern[1]	COSEWIC (2011)
	British Columbia	Blue[2]	BCCDC (2014)
United States	—	Species of Concern[3]	OBIC (2013)
	California	Species of Special Concern[4]	CNDDB (2014)
	Oregon	Sensitive – Vulnerable[5]	OBIC (2013)
	Washington	Forests and Fish Species[6]	FFR (2000)

[1] In the Canadian federal system, Special Concern is a watchlist category for wildlife species that may become threatened or endangered due to a combination of biological characteristics and identified threats.

[2] In the British Columbia provincial system, the Blue designation applies to any indigenous species or subspecies regarded as Special Concern (formerly Vulnerable). Taxa of Special Concern have characteristics that make them particularly sensitive or vulnerable to human activities or natural events, and are considered at risk, but are not Extirpated, Endangered or Threatened.

[3] Species of Concern is an informal term not defined in the federal Endangered Species Act; it is applied to a watchlist of species that appear to be declining or in need of conservation.

[4] Species of Special Concern is a vertebrate taxon native to California that satisfies one or more of the following criteria: 1) is extirpated from the State or, in the case of birds, from its primary seasonal or breeding role; 2) is listed as Federally-, but not State-, Threatened or Endangered; and meets the State definition of Threatened or Endangered but has not formally been listed; 3) is experiencing, or formerly experienced, serious (noncyclical) population declines or range retractions (not reversed) that, if continued or resumed, could qualify it for State Threatened or Endangered status; and 4) has naturally small populations exhibiting high susceptibility to risk from any factor(s), that if realized, could lead to declines that would qualify it for State Threatened or Endangered status.

[5] Sensitive – Vulnerable, one of four sensitive species categories used by the State of Oregon, consists of species facing one or more threats to their populations and/or habitats. Vulnerable species are not currently facing extirpation from a specific geographic area or the state but could become so with continued or increased threats to populations and/or habitats.

[6] Based on the Forests and Fish Report (2000; FFR), this was originally six stream-associated amphibians identified as potentially vulnerable to forestry practices. As the FFR was developed prior to partitioning tailed frogs into two species (Nielson *et al.* 2001), *A. truei* in Washington State included populations in the Blue Mountains later allocated to *A. montanus*. Partitioning added the seventh FFR Species.

Ascaphus truei currently has some status designation in every provincial and state-level political entity across its geographic range (Table 1). Status categories are not directly comparable among jurisdictions. However, except for Washington State, all designations for *A. truei* lack regulatory weight. Further, *A. truei* lacks a US federal designation, but has federal watchlist status (Species of Concern) in selected US Fish and Wildlife Service (USFWS) jurisdictions across portions of its geographic range. This pattern results in part from interaction with respective states, or federally circumscribed regions within states.

In Washington, *A. truei* is one of seven stream-associated amphibian species protected under the Forests and Fish Report *aka* Agreement (FFR). The FFR is a multi-stakeholder agreement addressing private and selected state timberlands that resulted in the 2006 FFR Habitat Conservation Plan (HCP), sometimes referred to as the Washington State HCP (WDNR 2009). Not all private timberlands in Washington State are addressed under this HCP (some, such as the Green Diamond Resource Company, have their own HCP), but the FFR HCP addresses over 3,763,576 ha (9,300,000 ac), which is a large majority of private timberlands and covers, to date, more area than any HCP in North America. The FFR HCP mandates that adaptive approaches be used to investigate the effectiveness of current regulations in protecting natural resources, among them *A. truei*.

In contrast to *A. truei*, designations for *A. montanus* are limited to the states of Oregon and Washington, and federal and provincial levels in Canada (Table 2).

TABLE 2. *Ascaphus montanus* status across its geographic range (November 2014).

COUNTRY	PROVINCE/ STATE	STATUS	SOURCE
Canada	—	Endangered[1]	COSEWIC (2013)
	British Columbia	Red[2]	BCCDC (2014)
United States	—	Species of Concern[3]	OBIC (2013), WDFW (2014)
	Idaho	No protective status	IDFG (2006)
	Montana	No protective status	MNHP (2014)
	Oregon	Sensitive – Vulnerable[4]	OBIC (2013)
	Washington	Forests and Fish Species[5] State Candidate[6]	FFR (2000) WDFW (2014)

[1] In the Canadian federal system, Endangered is applied to wildlife species facing imminent extirpation or extinction.

[2] In the British Columbia provincial system, the Red designation applies to any ecological community, and indigenous species and subspecies that is Extirpated, Endangered, or Threatened.

[3] Species of Concern is an informal term not defined in the federal Endangered Species Act; it is applied to a watchlist of species that appear to be declining or in need of conservation.

[4] Sensitive – Vulnerable, one of four sensitive species categories used by the State of Oregon, consists of species facing one or more threats to their populations and/or habitats. Vulnerable species are not currently imperiled with extirpation from a specific geographic area or the state but could become so with continued or increased threats to populations and/or habitats.

[5] Based on the Forests and Fish Report (FFR 2000), there was originally six stream-associated amphibians identified as potentially vulnerable to forestry practices. The FFR was developed prior to partitioning tailed frogs into two species (Nielson *et al.* 2001), at which time *A. montanus* in the Blue Mountains of Washington State represented part of *A. truei*. Partitioning added a seventh FFR Species.

[6] State Candidate is a fish or wildlife species that the Washington Department of Fish and Wildlife will review for possible listing as State Endangered, Threatened, or Sensitive.

In Canada, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) lists *A. montanus* as Endangered (Table 2). The initial COSEWIC assessment occurred in May 2000, before the two tailed frog species were partitioned. The assessment was done on the "Southern Mountain population" unit and COSEWIC was aware of its pending description as a species (however, see INTRODUCTION, BACKGROUND AND SYSTEMATICS section for lack of analysis collectively encompassing Canadian and US populations). Moreover, it is the responsibility of the federal government to legally protect species that COSEWIC designates under the Canadian Species at Risk Act (SARA). COSEWIC assessments do not address political, social or economic factors. Those factors must be assessed before a species can be included on SARA schedules, which affords it legal protection. On 5 June 2003, *A. montanus* became listed as Endangered in SARA Schedule 1, a designation that gave it full protection (D. Fraser, *pers. comm*.). In British Columbia, *A. montanus* has a Red designation (Table 2), which identifies at-risk taxa at provincial level needing investigation.

In Oregon and Washington, *A. montanus* has designations identical to *A. truei* except that *A. montanus* is also a State Candidate in Washington. The latter designation is based primarily on the fact that *A. montanus* has a very small portion of its geographic range in Washington.

LIFE HISTORY

Tanya Wahbe, Linda Dupuis, Marc Hayes, and Glenn Sutherland

The Seasonal Template

We partition tailed frog life histories into three periods: 1) the breeding season; 2) the non-breeding active season; and 3) the overwintering season. The unique life history of tailed frogs can result in temporal overlap between the first two periods because of individual and life stage variation. Both species of tailed frogs engage in internal fertilization that involves sperm storage for relatively long intervals (months to perhaps years; *A. truei*: Noble 1925, Noble and Putnam 1931, Sever *et al*. 2001; and *A. montanus*: Metter 1964b). Unlike other frogs in the PNW and elsewhere, this results in the temporal separation of breeding (coupling of adults) and oviposition (the laying of eggs; Brown 1975), a phenomenon that Jameson (1955) first pointed out. Hence, the basic approach to identifying the breeding season in tailed frogs is determining when adults are involved in amplectic (coupling) behavior. Thus, by definition, tailed frogs deposit eggs during the non-breeding active season.

The Breeding Season

Ascaphus truei: Unlike in many North American frogs (e.g., Berven 1981), distinct breeding migrations have not been reported for *A. truei*, in part because such migrations may be difficult to observe in their forested stream habitats. Most individuals trapped in fall streamside surveys in southwest British Columbia were upstream moving adults,[99] implying a breeding migration (Wahbe *et al*. 2000). Moreover, Hayes and colleagues

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[99] Wahbe and colleagues (2000) found 88% (n = 22) of *A. truei* recaptures during streamside to be moving upstream, and 47% (n = 16) of *A. truei* trapped were reproductive adults.

(2006) found that adult *A. truei* generally move upstream during summer and appear to locate near headwater origins in late summer-early fall. They speculated that richer food resources might drive the use of upstream habitats, but aggregation for breeding could also explain this pattern (Brown 1975). Whether adults display synchrony in these movements as reported for breeding migrations of some North American frogs (e.g., Berven 1981), and whether potentially long-lived adults (see *A. montanus* in next section) return to the same areas to breed annually is unstudied. Seasonal movement patterns should be a high priority for investigation, as these patterns are key to interpreting many aspects of tailed frog ecology, including potential responses to forest practices.

Breeding behavior of *A. truei* is distinctive in several ways. Males do not vocalize to attract females as the species is both voiceless (Noble and Putnam 1931) and lacks ear apparatus to detect relatively high frequency sounds (Noble 1931). Both sexes also have highly reduced lungs (Noble 1931), which have the secondary function of hydrostatic organs in other amphibians (Jorgenson 2000). In the flowing well-oxygenated aquatic habitat used by *A. truei*, well-developed lungs could make adults too buoyant to engage in their bottom-oriented searching behaviors (Noble and Putnam 1931). All amplectic pairs found in the field were found in water (Noble and Putnam 1931), a finding confirmed by later investigators. Males crawl along the bottom of mountain streams in search of females, a behavior that Noble and Putnam (1931) duplicated in the laboratory in aerated tanks with water 10 cm deep and chilled to between 5.7°C and 10.7°C. Despite the shallow depth of these tanks, reproductively ready males were not observed to come to the surface, but crawled along the bottom, using an alternating leg walk in their search for receptive females (Noble and Putnam 1931). This salamander-like movement is characteristic of *A. truei*, as the species is unable to execute parallel-leg swimming movements, like a frog kick (Abourachid and Green 1999), which reflects neural circuitry more similar to that of salamanders than that of other frogs. Some reproductively ready males, both in the field and in the lab, carry the cloacal tail directed forward during their bottom crawl (Noble and Putnam 1931). How male *A. truei* actually detect females beyond the near-visual range in the aquatic habitat is unknown, but some kind of smell-taste modality is suspect for frogs with salamander-like searching behaviors (Dawley 1998, Reiss and Eisthen 2008). In the laboratory, some reproductively ready males will seize any frog they come into contact with during their crawl (Noble and Putnam 1931). If the frog seized was male, it was released shortly thereafter; whereas if the individual was female, effort was made to improve its grip.

Based on the comments of Nussbaum and colleagues (1983), Stebbins (2003) described most breeding as occurring during early fall (specifically late August and September), but his comments are based on collective data for both tailed frog species.[100] Based on field observations of amplectic pairs made between 12 June and 6 July on the Olympia Peninsula near Lake Cushman, Noble and Phillips Putnam (1931) concluded that breeding was prolonged. They implied an even more prolonged breeding season with the observation of an adult male attempting to amplex a collecting bottle on 4 September. Based on information over her entire late June-early September sampling interval from the same area of the Olympic Peninsula, Gaige (1920) also concluded that breeding was

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[100] Stebbins (2003) did not provide a separate account for *A. montanus*, stating only that coastal and inland populations have been proposed as separate species.

prolonged, but her conclusion was based on recording males in breeding condition[101] rather than amplectic adults. Based on finding five adult males with well-developed secondary sex characters on 21 and 30 September and one amplectic pair on 1 October, Brown (1975) stated that mating occurs in late September and early October. He obtained these data from Razor Hone Creek, a northwest Washington montane stream (1,067 m [3,500 ft]). However, on the North Fork of the Mad River in northern California, mating is claimed to have been observed only in May, though males with secondary sexual characteristics have been observed in June and July (Sever *et al.* 2001); the seasonal effort that this assessment is based on is unclear. A few additional breeding observations exist for *A. truei* in March–May, but these involve individuals introduced into the same container following capture.[102] Metter (1967) believed that mating would not have taken place without manipulation. Specifically, Metter (1967) stated that male *Ascaphus* will clasp other individuals (male or female) anytime, regardless of the development of secondary male characters, if they are placed together in sacks or other containers. In early summer, he observed clasping sometimes continued for an hour or more, but the pairs always separated before copulation occurred. He suggested that the habit of the males of grabbing any individual that comes near them may be responsible for some reports of early season (May-June) breeding. Nevertheless, current data are too few to confidently characterize breeding season length, a peak breeding season (if any), or whether significant geographic variation exists in the breeding season (Data from Washington imply a prolonged season [at least summer-early fall], but the comments of Metter (1967) suggest the need for more study).

Many authors have contributed to understanding the internal fertilization breeding mode in *A. truei*. Van Denburgh (1912) described the distinctive male "tail", suggesting it was a sex organ. Van Winkle (1922), who first recognized its cloacal nature based on the position of the cloaca near its tip, repeated Van Denburgh's suggestion. Noble made key contributions through his discoveries of sperm in female oviducts, concealed cloacal spines that become visible as blood fills the breeding male "tail", and male ability to direct their "tail" forward and insert it into the female cloaca (Noble 1925, Noble and Putnam 1931). Of the over 6,400 currently recognized species of anurans, *A. truei* is the only species known to engage in copulation that includes intromission (Sever *et al.* 2001). In fact, coupling in *A. truei* has been termed copulexus due to the distinctive combination of amplexus with internal fertilization using the "penis-like" cloacal tail (Sever *et al.* 2001). Copulexus, which involves an inguinal or pelvic embrace[103] (Noble and Putnam 1931, Slater 1931, Metter 1964b, Wernz 1969), is a highly stereotyped behavior in which males may struggle for hours to gain the proper position before

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[101] Based on Gaige (1920), breeding males differ from non-breeding males in having enormously enlarged forearms (2-3 times normal size) and inner palmar tubercles; a white round horny patch on the forearm where the inner palmar tubercle contacts it when the arm is folded; and the inner palmar tubercle, the inner side of the first two fingers, and the round spot on the forearm are covered with black. Also, the underside of the "tail" is greatly congested; and the underside of the forearm is gray thickly dotted with white. Gaige (1920) also made her assessment of a prolonged breeding season based on females having large eggs, but this was prior to the understanding that breeding and oviposition were temporally separated.

[102] Slater (1931) reported on a 17 May mating of adults that had presumably recently emerged from overwintering in the Carbon River Valley (Mount Rainier National Park) and Wernz (1969) reported a few late March-early April matings from along the South Fork of the McKenzie River in Oregon.

[103] All other frogs native to the Pacific Northwest have pectoral or axillary amplexus or embrace.

achieving intromission[104] (Noble and Putnam 1931, Metter 1964b). Noble and Putnam (1931) thought that efforts of the male were directed toward maneuvering the female onto her back, in which position she typically entered a state of tonic immobility,[105] permitting the male to secure a grip. Metter (1964b) discounted this because he never saw it, but it seems consistent with the regular observation of upside down pairs of *A. truei* in the field in which the male has not yet achieved intromission (M. Hayes, *pers. obs*.; see also Bull and Carter [1996a] and Stephenson and Verrell [2003] for *A. montanus*). After the male achieves a pelvic grip, the female extends her hind limbs so that they form a narrow V (Noble and Putnam 1931, Slater 1931, Metter 1964b, Wernz 1969). Metter (1964b) thought that this behavior represented female rejection of the male, but Wernz (1969) showed that it helped guide the male's cloacal tail to achieve intromission. Once intromission was achieved, both male and female folded their hindlimbs up to the normal resting position (Metter 1964b, Wernz 1969). The manipulated observations of Wernz (1969) and Brown (1975) also imply that copulectic *A. truei* remained paired for long intervals. Wernz (1969) described paired *A. truei* kept in the laboratory at 7°C as lasting 70 hr, whereas Brown (1975) placed a coupled pair removed from the field in a refrigerator a 4°C, where they remained coupled for 7 more days.

Ascaphus montanus: Breeding migrations for *A. montanus* are also unreported. In fact, adult *A. montanus* seem to display high site fidelity or philopatry and as such, were regarded as sedentary (Daugherty and Sheldon 1982a). These data need to be interpreted cautiously because Daugherty and Sheldon (1982a) may have missed the seasonal movement interval; movements of adult *A. montanus* have been recorded outside the interval that Daugherty and Sheldon sampled (Adams and Frissell 2001). Based on few data, Metter (1964a) suspected that adults moved because he observed numerous adult tailed frogs on the mainstem North Fork Touchet River in spring, but few adults at that location in late summer. He toe-clipped 75 adults on the lower portion of one creek near the mainstem, but recaptured only two of these animals, each only a few meters from their release point. Adams and Frissell (2001) recorded a fall move of adults in one of two streams, which they believed was linked to temperature. Whether that move was also associated with breeding is not known.

Metter (1964a), who studied *A. montanus* along the North Fork of the Touchet River at 1,158 m (3,800 ft) and on White Pine and Eldorado Gulches on the North Fork of the Palouse River at 975 m (3,200 ft), indicated that breeding occurs in early fall, basically September-October. Metter (1964a) inferred breeding in the field from changes in male secondary sexual characteristics that become prominent only during breeding season,[106]

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[104] Noble and Putnam (1931) noted that, "In the field, mating pairs have been kept under observation for twenty-nine hours. Further, most mated pairs were first observed near noon and presumably some had been struggling since the previous evening for *Ascaphus* does not move above until nightfall." However, it is unclear from their statements whether a mating pair simply meant a male in a pelvic embrace or in copulectic posture. Metter (1964b) also notes that, "…attempted mating…often lasted for 48 hr."

[105] A female maneuvered onto her back typically remains quiet whether or not a male continues to attempt amplexus (Noble and Putnam 1931). Noble and Putnam (1931) mention a female that remained on her back for 22 min after the male has disengaged.

[106] This includes warts edging the chin, cloacal spines, nuptial (thumb and forearm) pads, and tubercles on the chest (Metter 1964a). Metter (1964a) recorded marked seasonal changes in these features, which reached their greatest intensity in October. In May-June, nuptial pads were white; they were gray by mid-July and black and horny by September; this intensified into October, but declined thereafter.

and from the mating behavior of adults kept in the laboratory[107] (Metter 1964b). Mating attempts, most of which were unsuccessful, were first observed on 6 September and continued until 19 October (Metter 1964b)[108]. Males grabbed any animal, regardless of reproductive readiness. In the laboratory, Metter (1964b) recorded males[109] in copulexus eight times over the interval 4 September-3 October. Development of the secondary sexual characteristics was not associated with the shortened length of fall days because captive males developed those characters at the same time as animals in the field despite lack of exposure to outside light (Metter 1964b). By mid-November, males showed no evidence of reproductive activity. Metter never observed copulexus in the field.

Bull and Carter (1996*a*) encountered five mating pairs[110] during fieldwork in the Wallowa Mountains of northeastern Oregon. Three were found clasping,[111] floating upside down on 17, 18 and 20 August; in each case, the male's "tail" was not inserted in the female's cloaca. Two pairs clasping in an upright position in full copulectic posture (i.e., male tail inserted) were found under rocks on 17 September and 5 October.

Based on laboratory observations and manipulative experiments, Stephenson and Verrell (2003) studied the mating behavior of *A. montanus* using adults obtained at Mountain Gulch, a headwater tributary of the North Fork of the Palouse River. They confirmed the basic aspects of copulectic behavior reported for *A. truei*. They also found that males seemed to respond visually to other adults by swimming toward them rapidly, and tactile contact via clasping preceded most mating attempts. Typically, some kind of clasp was a precursor to amplexus, though males occasionally amplexed females without first clasping them. Females were occasionally flipped onto their backs when clasped, or during amplexus or copulexus, but this seem neither intentional nor directed (*contra* Noble and Putnam [1931] for *A. truei*.). Though dorsal amplexus was the usual inguinal amplectic posture, ventral amplexus[112] was observed 10 times in the laboratory and once in the field. The insertion of the male's tail to achieve copulexus always occurred during amplexus. Stephenson and Verrell (2003) also observed hindlimb kicks to be common during copulexus; kicks did not move the mating pair, they were variable in frequency, and they may stimulate the female tactually. This behavior differs from the description of

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[107] Metter (1964b) maintained adult *Ascaphus* in plastic cartons at 10°C [50°F] in a dark refrigerator in a "considerably lighted" room. These data are based on a composite of individuals of *A. montanus* from Idaho and Washington, and *A. truei* from the east slope Cascades. Due to the mode of presentation, one cannot partition these data into observations attributable to *A. montanus* versus *A. truei*, but we present these data because some of it may assist understanding *A. montanus* reproductive behavior.

[108] Metter (1964b) observed that when a male grabbed a female, either by the body or legs, she frequently extended her legs in the narrow V, but he never observed the completion of mating with the female in that position. He thus concluded that females assume this tonic posture to reject males, but Wernz (1969) indicating that it helps guide the *A. truei* male toward the cloacal to achieve intromission indicates that either *A. montanus* displays different behavior, Metter somehow missed entire behavioral sequence, or females that Metter saw display the narrow V behavior were rejecting males on other bases that he did not recognize. During these attempted matings, which often lasted for 48 hr, the cloacal tail was directed forward and purple, indicating it was engorged with blood. Metter (1964b) never observed a male maneuver a female onto her back, as Noble and Putnam (1931) described for *A. truei*.

[109] Only those with well-developed secondary characteristics.

[110] Bull and Carter (1996a) actually found six pairs of coupled tailed frogs, but one was a male-male pair.

[111] Bull and Carter (1996a) using clasping to mean inguinal or pelvic amplexus, whereas Stephenson and Verrell (2003) used in it to mean that the male places at least one forelimb around the limbs or body of the female.

[112] Stephenson and Verrell (2003) described this belly-to-belly posture as the venters of the pair contacting one other in apposition. The male's forelimbs wrap around the female anterior to her pelvic region and may interlace on her dorsum.

Noble and Putnam (1931) for *A. truei*, who described mating male *A. truei* as motionless, but may be similar to the description of Wernz (1969), who noted that male *A. truei* occasionally gave slight thrusts during copulexus.

In summary, *A. montanus* may typically be a fall breeder, but more complete seasonal data from different locations across its range are needed for confirmation, and telemetry data will likely be needed to establish movement patterns. The true context of movement in *A. montanus* is currently uninterpretable. As with *A. truei*, seasonal movement patterns should be a high priority for investigation.

The Non-Breeding Active Season

The non-breeding active season encompasses different intervals depending on whether adult or non-adult life stages are addressed. For adults, it encompasses the entire active-season exclusive of the breeding interval; for non-adult life stages, it includes the entire active-season interval.

Oviposition and Embryonic Development: Oviposition and embryonic development begins with behaviors leading to oviposition and ends with larvae emerging at hatching. Since females can store sperm and breeding and oviposition occur at different times, unlike most other frogs, only females engage in oviposition.

> *Ascaphus truei*: Brown (1975) thought that female *A. truei* in northwestern Washington move upstream into small shallow tributaries of a mainstem creek during July and there deposited eggs near the end of July. However, his proposal is difficult to evaluate because Brown (1975) presented no actual movement data and he described the spatial scale of his field effort only in general terms. Further, of the few field clutches (number unspecified) that Brown (1975) found, one was in the mainstem creek downstream of small shallow tributaries. Hayes and colleagues (2006) believed females had to move downstream to deposit eggs, since adults were located near headwater stream origins in late summer-early fall and egg masses were found several hundred meters downstream in the same systems. Further, their observation of adults near headwater stream origins in late summer-early fall implies that any movement downstream to reach oviposition sites had to occur outside that interval (Hayes *et al.* 2006). If the upstream to tributary movement hypothesis of Brown (1975) is correct, the basis of the difference with the observations of Hayes and colleagues (2006) is unclear. The downstream movements to oviposition sites that Hayes and colleagues (2006) inferred is based on data from the Willapa Hills of southwestern Washington, where surface flow near headwater stream origins is often seasonal or spatially intermittent and dependent mostly on rain-fed groundwater (versus snow; Hunter *et al*. 2005). This hydrology may differ from snow-dominated systems such as Brown's (1975) study area in northwestern Washington. Similar to movements associated with breeding, we know little about movements of females associated with laying eggs. Both types of behaviors deserve attention because of factors, such as forestry practices, that have the potential to change movement patterns.
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> Though Brown (1975) only speculated about upstream movement of female *A. truei*, he provided information on their seasonal aggregation beneath rocks, a phenomenon that had not been previously described. In particular, he found aggregations of 6 and 7 on 13 July 1968, groups of 5 and 8 on 1 July 1969, and an aggregation of 20 females under

one rock on 23 July 1972 (Brown 1975). A presumptively communal oviposition site[113] with 123 embryos in early cleavage stages was located at the point where the last aggregation was observed (Brown 1975). The spatial relationship between aggregations was not reported. Similarly, on the eastern Olympic Peninsula of Washington State, Amber Palmeri-Miles and colleagues (2010) observed an ovipositing female with three spent females and a gravid one within a small area of stream (ca. 1 m) roughly 2 km below the stream origin on 29 July 2008.

Before ovulation, liver-stored fat is the energy source female *A. truei* mobilize into yolking eggs. Based on macroscopic and histological examination of 32 adults (female and male) collected from two Oregon populations,[114] Belton and Owczarzak (1968) showed that post-overwintering females with only partly developed ova doubled their liver mass. Lipids and carotene pigments from this accumulation gave the liver a bright yellow appearance and soft consistency, whereas livers of male *A. truei* remained the typical dark brown. However, the obvious sexual dimorphism in liver size and appearance in females was lost prior to ovulation as females mobilized lipids into eggs. Belton and Owczarzak (1968) clearly describe the pre-to-post ovulatory change in liver morphology. However, they did not report the date of their post-ovulatory sampling relative to oviposition and thus, it is difficult to translate the process into a timeline for the two populations they studied. Moreover, as their animals came from relatively low elevation populations in Oregon, their work should be viewed as an initial glimpse into the process that may not translate the same way across *A. truei* geographic range.

Deposition of eggs is thought to occur the year following mating (Brown 1975).[115] Gaige (1920) reported two bunches[116] of eggs laid in MacTaggert Creek[117] on 5 August. She gave no development stage, so oviposition may have taken place in July or early August. Gaige (1920) also speculated that the oviposition season[118] was between 27 June and early September based on finding female *A. truei* containing large eggs. Noble and Putnam (1931) found females with distended ovaries throughout July, a condition which reflects imminent oviposition (Sever *et al.* 2001).[119] Brown (1975) reported oviposition in mid-to-late July. Snowmelt can markedly influence the

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[113] This oviposition site was presumptively communal because the total number of embryos was 27 more than the maximum clutch size reported for the species (n = 96; Bury *et al.* 2001) and the total number of embryos was nearly triple that of the mean clutch size for the species across its geographic range (n = 42; Karraker *et al.* 2006).

[114] Belton and Owczarzak (1968) collected *A. truei* from Mary's Peak (Benton County) and the south fork of the McKenzie River (Lane County).

[115] Egg may be fertilized by sperm from mating the previous year. Sever and colleagues (2001) found sperm in the oviducts of both vitellogenic and non-vitellogenic female *A. truei* obtained in June and July from northern California. When those sperm were acquired is unknown, but non-vitellogenic females would not have laid eggs until the following year. Actual sperm storage capabilities of female *A. truei* need experimental verification. Existing data do not exclude the possibility of oviposition of eggs fertilized in the same year.

[116] Gaige (1920) brought the eggs in from the field, where they continued to develop until 13 August, at which time she was forced to preserve them due to lack cold water to maintain them. She also described the egg strings as so entangled that it was impossible to count them. Hence, from her description, it is not possible either to estimate clutch size, understand whether either bunch of eggs represented more than one clutch, or understand whether both bunches were from the same stream.

[117] McTaggart Creek (the MacTaggert Creek of Gaige [1920]) is a tributary of the North Fork of the Skokomish River just south of Lake Cushman.

[118] Gaige (1920) used the term breeding season, but this was prior to understanding of the partitioning between breeding *sensu stricto* and oviposition.

[119] Noble and Putnam (1931) used females with distended ovaries as support for what they termed the prolonged breeding season, but this was also prior to understanding of the temporal separation between breeding and oviposition.

hydrographs of higher elevation streams similar to the ones that Brown (1975) studied. Thus, *A. truei* populations that occupy these types of streams may be constrained as to how early oviposition may occur. Adams (1993) found 27 late-stage embryos at an oviposition site with 33 newly hatched larvae on 12 August; the degree of development implies oviposition sometime in July. Adams (1993) also commented on a clutch found by Paul Corn on 19 July in Lost Creek, Oregon. Though no developmental stage was indicated, based on developmental rates (Brown 1975) at the reported stream temperature of 13°C, oviposition would have occurred in early July.[120] Karraker and Beyersdorf (1997) found an oviposition site in the MacDonald Creek drainage (coastal northern California) on 16 August with 28 eggs. Oviposition at this site likely occurred in early August based on the fact that recently hatched larvae were observed in the pool below the oviposition site by 26 August and a water temperature of 15.9°C was reported at 17:00 hr on 16 August. Bury and colleagues (2001) reported on six *A. truei* oviposition sites found 8 July-15 August, and concluded that oviposition occurred in early July to early August, based on developmental information and stream temperatures. Most recently, Palmeri-Miles and colleagues (2010) observed a female *A. truei* laying eggs on 29 July along with three other egg masses that were likely laid just days earlier.[121] Karraker and colleagues (2006) estimated oviposition timing, based on developmental data of Brown (1975), for 28 *A. truei* clutches across much of the geographic range for which date, developmental stage, and water temperature existed at the time of the find. They estimated oviposition dates ranging from 10 June to 29 August ($\bar{x}$ = 24 July), and found that that elevation explained more than 25% of the variation in oviposition timing ($r^2 = 0.26$, $P < 0.01$). No relationship was found between *A. truei* oviposition timing and latitude ($r^2 = 0.03$, $P = 0.37$), longitude ($r^2 < 0.01$, $P = 0.88$), or water temperature ($r^2 = 0.12$, $P = 0.07$). However, the effect of water temperature may be worth further investigation, especially because elevation and temperature are correlated (Dodson and Marks 1997) and amphibians in general display a progressive delay in breeding with elevation (Morrison and Hero 2003). In summary, *A. truei* generally deposit eggs in summer, but investigation of how the timing of oviposition changes with elevation, hydrographs, and temperature is needed.

The white unpigmented eggs of *A. truei* are the largest among North American frogs (FIGURE 4), but few reports of their size exist. In a general description, Gaige (1920) reported capsular and yolk[122] diameters for eggs of 8 and 5 mm, respectively. More precise measurement of an unspecified number of eggs gave a mean of 4.0 mm (range 3.7-4.5 mm; Brown 1989). However, these eggs were obtained via hormonal induction, so they may not reflect the sizes of eggs found in the field. Adams (1993) reported a mean egg diameter of 6.1 mm (range 4.7-7.1)[123] for the clutch from Curry County, Oregon, and indicated that the clutch that Corn found in Douglas County had eggs

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[120] Determination of this oviposition date assumes that water temperatures were near 13°C from the time of ovipositon to when the mass was found, as the estimates Brown (1975) were based on rearing at a constant temperature. If temperatures over some of the interval were cooler, oviposition could have occurred in late June. This determination also assumes that *A. truei* from Douglas County Oregon do not different substantially in their developmental pattern from their counterparts in northern Washington.

[121] These observations were made on Miller Creek, which is located on the eastern Olympic Peninsula that drains directly into Hood Canal (Palmeri-Miles *et al.* 2010).

[122] Yolk diameter is the diameter of the ovum proper; capsular diameter is the diameter of the jelly capsule surrounding the egg or ovum.

[123] Egg diameter values of Adams (1993) were obtained after preservation.

averaging 6 mm in diameter. Adams (1993) does not indicate whether diameters are capsular or ovum measures. Given data on other anurans, variation in egg size is expected, but data are currently lacking to assess this in a systematic way.

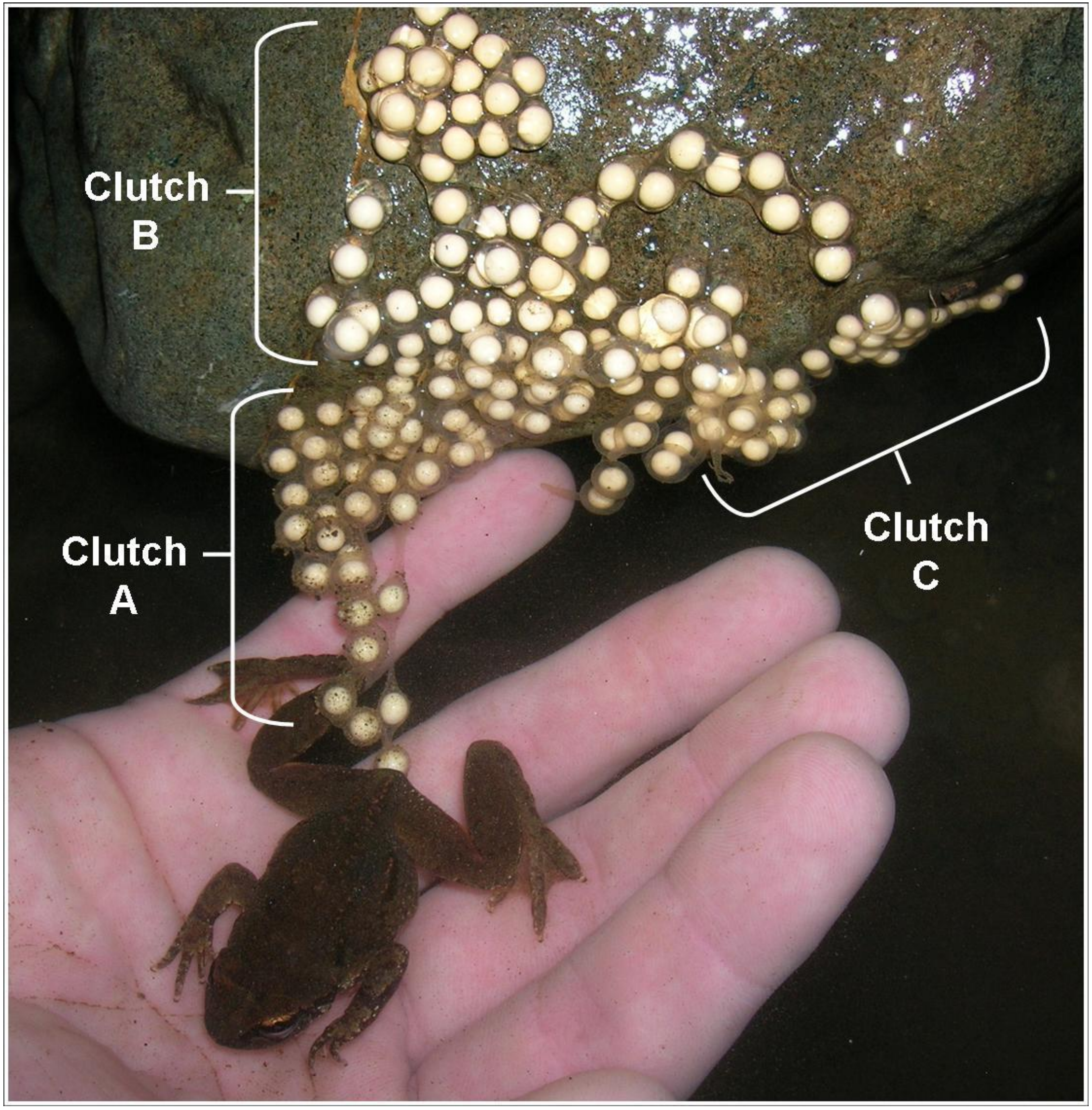

FIGURE 4. Female *A. truei* in the process of depositing eggs (adapted from Palmeri-Miles *et al*. [2010]).

Besides the clutch that the female is depositing (A), two additional clutches of eggs (B and C) have already been deposited on the rock. (Photograph credit: Keith Douville)

Eggs are deposited in paired strands on the undersurfaces of instream rocks (FIGURE 4), though descriptions of their appearance are sparse. Gaige (1920), the first to find *A. truei* egg masses, described two "bunches", although it was unclear whether more than one clutch was represented. She described them as, "…laid in a rosary-like string twisted about to form a large circular mass which was attached to the lower surface of the stone." Brown (1975) described other aspects of eggs and egg masses, but not the clutches he found in the field. Adams (1993) described a mass with late development embryos as in "broken strings" beneath a boulder; the fragmented aspect of this description may be typical of egg masses late in development, as the jelly across the narrow connections between egg capsules may be the first to break down. The mass that Corn found (Adams 1993) was described as consisting of "…a single string but in a mass measuring 35 × 55 mm…" under a 23 × 17 cm rock. Eggs in this mass averaged 6 mm in diameter, so the single string had to have been folded back on itself multiple times to be so compact. Further, if this mass was really in a single continuous string, then female *A. truei* may sometimes deposit the complement of eggs from only one of their ovaries rather than both, as is typical in anurans. The clutch description that Karraker and Beyersdorf (1997) provided, "…25 eggs…in a loose string [singular] beneath the boulder" also suggests this possibility. Bury and colleagues (2001) described all but one of six clutches or clutch groups as "congealed into a mass". The exception was a mass found in the Skokomish drainage, which had, "…96 newly deposited eggs still in a rosary-like string and attached at one end to the underside of a rock (the loose end flowed into the dipnet when the rock was turned)." Whether this mass was in a more "congealed" configuration prior to the rock being turned is unknown. The peculiar aspect of this account is the description of the singular egg string because this clutch is thought to represent the maximum clutch size known for *A. truei*. Either the "one string" terminology was loosely used, the female that deposited these eggs was laying a huge complement from only one ovary, or we misconstrue the oviposition pattern in *A. truei* so that egg strings from two separate ovaries can be made to look like one when laid. Karraker and colleagues (2006) provided a rangewide summary of two important structural aspects of the description of *A. truei* oviposition sites: the substrate to which egg masses were attached (as a standard clast size) and the aquatic microhabitat (as cascade, riffle, run, or pool). Of 32 oviposition sites where substrate data were available, all but two were on cobbles (n = 18) or boulders (n = 12); of the exceptions, one was on gravel and the remaining one did not apply since it involved detached eggs (original attachment substrate unknown). Of 34 oviposition sites with aquatic microhabitat data, all but three were in riffles (n = 18) or pools (n = 13); two of the three exceptions were in a cascade and one was in a run. In summary, most descriptions of oviposition sites have been too general to really improve on the understanding of the typical appearance of a clutch or its microhabitat. Use of larger clasts (cobbles and boulder) may simply reflect the requirement of having enough concealed and sheltered area to which to attach an egg mass.

Karraker and colleagues (2006) summarized available information on *A. truei* clutch size. Mean clutch size across the geographic range was 41.9 (SD = 16.3; range: 20-96). Clutch size of 24 presumptively single clutches was not related to elevation, latitude, and longitude (elevation: $r^2 = 0.02$, $P = 0.52$; latitude: $r^2 = 0.09$, $P = 0.15$; longitude: $r^2 = 0.01$, $P = 0.98$). However, as with oviposition timing, small sample size and the low P value for the relationship between clutch size and latitude suggests that latitude may be worth re-investigation as more data become available. Karraker and colleagues (2006) also summarized *A. truei* clutch size data from a combination of previous data on dissections of gravid females and induced ovulations. These data, based on 85 females from across the range in Washington and Oregon, reveal a mean clutch size of 57 (range: 28-98). These data are not directly comparable with field data because much of the latter data are based on population summaries rather than individual clutches. However, the difference may reflect geographic discordance between the samples, inclusion of eggs insufficiently developed to be laid that year, or egg retention and/or resorption of eggs that could be laid prior to oviposition. Further, if *A. truei* females can deposit eggs from only one of their ovaries, then the variance in clutch size would increase substantially if populations used both modes of oviposition. Lastly, though Gaige (1920) did not provide data on clutch size, she provided ovary-specific counts of developed eggs on two of the females she collected; these suggest a high degree of symmetry in ovarian egg development (one female had 16 eggs in the left ovary and 17 in the right; the other had 24 in the left and 25 in the right).

Some evidence exists for variation in clutch frequency, i.e., how often a female can lay eggs. Though it is unclear precisely how fast female *A. truei* can yolk up eggs, a slow developmental physiology (Brown 1975, 1989) makes it likely that the process is slow. Moreover, it is unclear whether the two-month oviposition season is a general pattern or that actual season length is shorter at a particular location (Karraker *et al.* 2006). Even if oviposition season length is typically two months, this is undoubtedly too short to allow multiple clutching. Metter (1967) presented evidence for *A. truei* females laying eggs every other year except in two populations. Females about to lay eggs in a particular summer can generally be distinguished from non-laying females externally and internally. A few weeks prior to the oviposition season, females due to deposit eggs develop thick black cornifications on the tips of all digits. Internally, these females will have developing eggs 3.5-4.5 mm in diameter in early summer. Ova are about 4.5 mm when laid in July. Post-oviposition, the ovaries have only undeveloped eggs for several weeks, which then shrink as the next clutch begins developing. In females not laying eggs during a summer, the ova are <2.5 mm in early summer and develop to a maximum of about 3.5 mm by late fall. Metter (1967) also found laying and non-laying females in a ratio of 1:1 in all populations where both conditions were recorded. Two studies provide some support for the idea that females lay eggs every year. Metter (1967) studied *A. truei* on the Hamma Hamma and Toutle Rivers (Washington) and found but a single reproductive female group and speculated that females in these populations might lay every year. While Burkholder and Diller (2007) indicated that northern California *A. truei* suggested a biennial reproductive cycle, one female captured during the oviposition period in consecutive years reproduced in both years. Thus, a possibility exists for a latitudinal cline in reproductive frequency in *A. truei*, especially if a larger range[124] were evaluated (J. Richardson, *pers. comm.*).

Ascaphus has been described as having the longest interval of embryonic development of any North American frog (Brown 1975). This assessment is based on rearing of eggs from montane northwestern Washington at constant temperatures across the range of temperatures where *A. truei* is thought to be capable of normal development (5-18°C [41.0-64.4°F]); Brown 1975). It is unclear if 5°C (41°F) is the real lower temperature limit because one of Brown’s (1975) two trials at 5°C (41°F) had 90% survival while the other had only 10% survival. If one accepts 5°C (41°F) as the lower limit, embryonic development at that temperature requires nearly 11 weeks, while embryonic development at 18°C (64.4°F) requires slightly under 11 days. In the range of stream

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[124] Metter (1967) data were only from Oregon and Washington.

temperatures where Brown (1975) conducted his fieldwork (7.6-11.0°C [45.7-51.8°F]), embryonic development would require 3 to 6 weeks. Brown (1975) also noted that developmental rates were much more responsive to temperatures at the lower end of this range than the higher end (5-10°C [41.0-50.0°F], temperature coefficient[125] (Q_{10}) = 8.6; 10-15°C [50.0-59.0°F], Q_{10} = 4.3; 15-18°C [59.0-64.4°F], Q_{10} = 1.8).

Brown (1975) considered the critical thermal maximum for *A. truei* embryos to be ~18.5°C (65.3°F). This was based on his constant-temperature developmental trials at 18.0°C (64.4°F) exhibiting 100% survival and those at 19.0°C (66.2°F) having just 26% survival. However, field temperature data from both *A. truei*-occupied streams and *A. truei* oviposition sites rarely if ever approached this temperature. Karraker and colleagues (2006) summarized temperature data at oviposition sites (n = 35), and showed that only three had temperatures ≥14.0°C (57.2°F) (the highest was 15.9°C [60.6°F]), and all three were located at the southern end of *A. truei* range in northwestern California or extreme southwestern Oregon. Temperature data for *A. truei*-occupied streams also indicated broad temperature variation below 18.0°C (64.4°F; Karraker *et al.* 2006). Survival rates of *A. truei* eggs from field data are unavailable.

Outside of the temperature experiments of Brown (1975), almost no data exist on the mortality factors affecting embryos prior to hatching. Brown (1989) speculated that the concealed mode of oviposition contributed to reducing the predation risk and accidental death from the physical stresses of the stream environment. If the latter is true, we would expect oviposition at locations and over time intervals where bedload movement is limited or non-existent. Such a hypothesis remains unexamined. Nussbaum and colleagues (1983) commented that Cope's giant salamander (*Dicamptodon copei*) ate the eggs of *Ascaphus truei*, but provided no data to support this comment. The impact of predation on *A. truei* eggs is not known.

Ascaphus montanus: Though Daugherty (1979) marked several hundred *A. montanus* over five years during demography studies on the species, he did not detect movement of females associated with egg deposition. The only significant movements reported for adult *A. montanus* have occurred outside the presumed oviposition season (Adams and Frissell 2001; see subsequent discussion on *A. montanus* oviposition). Nonetheless, no studies of *A. montanus* have been designed to focus explicitly on *A. montanus* adult movement.

As with *A. truei*, deposition of eggs is thought to typically occur the year following mating (Metter 1964b).[126] Few egg clutches of *A. montanus* have been found, and some oviposition dates have been inferred from data other than direct field observation of

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[125] The temperature coefficient (Q_{10}) represents the factor by which the rate (R) of a reaction increases for every 10-degree rise in the temperature (T). The rate (R) may represent any measure of the progress of a process.

[126] As with *A. truei*, *A. montanus* eggs are believed to be fertilized by sperm from mating the previous year. Evidence that Metter (1964b) provided for sperm storage was based on examination of the reproductive tract of 19 adult females collected in the fall. Fifteen females had sperm in the lower (uterine) tract, but not in the upper (coiled) tract. Uterine and oviduct walls may supply nutrients. Females lacking sperm and those that bred in the lab had swollen fatty tracts, a condition independent of fat body size. Females with sperm but that had not bred in the lab had thinner-walled tracts with little fat. Metter (1964b) was not able to determine whether females mate every fall or if sperm can remain viable for more than a year. Three females collected in September 1963 with 0.8-1.3 mm diameter eggs contained sperm though they were not due to lay until July 1965. This could imply sperm viability for 2 years if these females did not remate in the fall of 1964.

eggs. In the Palouse (Idaho) and Touchet (Washington) areas, Metter (1964a) inferred that the laying season extended from late June to early August based on his observation, only during that period, of females with ovaries so distended that eggs could easily be seen through the body wall. Franz (1970a), the first to describe *A. montanus* eggs in the field, found two clutches of eggs on 20 July. Similar to Metter (1964a), Daugherty and Sheldon (1982a) inferred oviposition through observation of females,[127] and indicated that oviposition began in June and roughly coincides with the end of spring runoff. They suggested that this timing minimized destruction of eggs by high flows. Karraker and colleagues (2006), summarizing data on 24 *A. montanus* clutches, estimated that eggs were laid over the interval 24 June-27 July ($\bar{x}$ = 7 July), and found that water temperature explained 22% of the variation in oviposition timing ($r^2 = 0.22$, $P = 0.02$). No significant relationship[128] was found between *A. montanus* oviposition timing and elevation ($r^2 = 0.15$, $P = 0.06$), latitude ($r^2 = 0.06$, $P = 0.25$), or longitude ($r^2 = 0.05$, $P = 0.34$). The relationship between oviposition timing and elevation deserves re-examination given the well-known relationship between elevation and temperature.

Eggs of *A. montanus*, an unpigmented creamy white, are similar to those of *A. truei*, but only one report of their size exists. In a general description, Franz (1970a) reported a yolk diameter of 4 mm. Size was based on eggs at or approaching the late gastrula embryonic stage, when the eggs are still spherical in appearance.

As with *A. truei*, eggs are deposited in paired strands on the undersurfaces of instream rocks, though descriptions are similarly sparse. Franz (1970a) described two clutches that they were attached in double strands to the underside of a large triangular boulder in a small waterfall. The masses, described as globular, were suspended in a small water-filled depression so that water percolating down among several large rocks circulated around the eggs. Karraker and colleagues (2006) summarized the substrate to which *A montanus* egg masses were attached and the oviposition microhabitat. Of 18 oviposition sites with substrate data, 12 were on boulders, five were on cobbles, and one was on gravel. Of 19 oviposition sites with aquatic reach data, 16 were in riffles (n = 16); two of the remaining three were in cascades and one was in a pool. More frequent use of boulders may simply reflect the larger average clutch size in *A. montanus* when compared to *A. truei* (Karraker *et al.* 2006).

Karraker and colleagues (2006) summarized available data on *A. montanus* clutch size. Mean clutch size across the geographic range was 66.6 (SD = 29.6; range: 41-150). The number of eggs in 15 presumptively single clutches was not related to elevation ($r^2 = 0.06$, $P = 0.40$), latitude ($r^2 < 0.01$, $P = 0.95$), or longitude ($r^2 = 0.15$, $P = 0.15$). Karraker and colleagues (2006) also summarized *A. montanus* clutch size data from a combination of previous data on dissections and induced ovulations. These data, based on 88 females from across the range in Oregon, Washington, Idaho and Montana, reveal a mean clutch size of 65 (range: 33-97). As with *A. truei*, these data are not comparable with clutch data from oviposition sites because much of the latter data were only available as population summaries. However, the difference may reflect

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[127] Similar to Metter (1964a), Daugherty and Sheldon (1982a) assessed female reproductive condition by observation of the sizes of the egg groups and individual eggs visible through the transparent abdominal wall and the condition of the fingertips.

[128] Based on $\alpha = 0.05$.

geographic discordance between the samples, inclusion of eggs insufficiently developed to be laid that year, or egg retention and/or resorption of eggs that could be laid prior to oviposition. Clutch size in *A. montanus* is significantly larger than in *A. truei*, regardless of whether clutch size data come from the field or dissections/induced ovulations (Karraker *et al.* 2006).

Evidence exists for variation in clutch frequency. Metter (1964b) found that 19 females dissected in late November[129] fell into 2 groups based on egg size (10 had larger eggs [2.9-3.3 mm in diameter] and 9 had smaller eggs [0.8-1.3 mm in diameter]). Females with the larger eggs would have laid the following year, whereas females with the smaller eggs would have deposited eggs two years later. Metter (1964b) did not relate female body size to these egg size groups of females, so it is unclear whether females with smaller eggs were younger or reproduce every other year. Daugherty and Sheldon (1982a) had stronger confirmation of biennial reproduction among females at a population at Bulter Creek, Montana, where animals had been individually marked for population studies. Sizes of the egg group and individual eggs visible through the semi-transparent ventral abdominal wall and the condition of the fingertips were used to determine the reproductive condition of females.[130] Sequential records of the reproductive condition of all 38 mature females captured in consecutive years verified the biennial reproductive cycle.

Few data on the embryonic interval are available for *A. montanus*. Metter (1964a) suggested that his observations from Touchet and Palouse Creeks were similar to the Noble and Putnam (1931) observation that eggs required one month to hatch in the laboratory. Since he observed no *A. montanus* clutches in the field, it is unclear how Metter determined that value. We suspect that Metter may have inferred it from the difference in time when he first observed gravid females versus hatchling larvae in the field. On 20 July 1968, Franz (1970a) translocated eggs from an *A. montanus* clutch obtained at Twelve-Mile Creek at 1,250 m (4,100 feet), a tributary of the St. Regis River drainage[131] in northwestern Montana to a small stream near the University of Montana's Biological Station at Yellow Bay, Flathead Lake. At the time of collection, the Twelve-Mile Creek eggs were at or approaching late gastrula (embryonic stage) in water 11ºC. Translocated eggs[132] were placed in a nylon stocking within a screened box to ensure adequate flow in the recipient stream, which was described as having similar chemical and thermal properties as the donor stream.[133] Hatching occurred over 3-5 September (46-48 days [6.6-6.9 weeks] later). Given the stage at which eggs were first

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[129] The collections of Metter (1964b) were from northern Idaho, the Blue Mountains of Washington, and the east slope of the Cascades. He did not partition the individuals from these areas in his discussion, so the reproductive sample upon which he reported may be a composite of *A. montanus* and *A. truei*.

[130] Daugherty and Sheldon (1982a) indicated that females captured prior to egg-laying in June had a large, clearly visible mass of bright yellow eggs, and their fingertips were black (see also Metter 1964b). Immediately after laying, no eggs were visible, but the black fingertips persisted through mid-July. By late August, small yellow eggs became visible. During the next summer, eggs continued to develop and were clearly larger than the previous year. By late August, the eggs were extremely large, and it became apparent that, following mating in August-September, the eggs would be laid the following June.

[131] The St. Regis River drainage is a tributary of Clark’s Fork, a major tributary of the Columbia River.

[132] Translocation from St. Regis to the recipient stream near the biological station was done with styrofoam ice chest and completed within 5 hours.

[133] Spot data from the stream of origin of this egg mass showed a pH of 7.2, dissolved oxygen of 11.2 parts per million (ppm = milligrams/liter [mg/L]), free carbon dioxide of 3 ppm [mg/L], bicarbonates of 28 ppm [mg/L], and no recordable carbonates. No parallel data were provided for the donor stream.

found, this underestimates the time required to incubate eggs at a water temperature close to 11ºC. Brown (1975) showed that *A. truei* eggs incubated at a constant 11ºC took 22.6 days (3.2 weeks) to hatch, so incubation of *A. montanus* eggs may be less than half as fast. Whether this relationship remains similar at higher stream temperatures, which occur frequently in *A. montanus* habitat (Dunham *et al.* 2007), is unclear. Survival rates of *A. montanus* eggs through the incubation interval are not known from field data.

Karraker and colleagues (2006) estimated the timing of hatching in *A. montanus* as ranging from 30 June to 17 September ($\bar{x}$ = 14 August). However, these estimates should be regarded as preliminary since the dates were estimated from developmental regressions based on *A. truei* that were laboratory-reared under constant temperature regimes. Further, both the somewhat lengthy developmental interval suggested by Franz (1970a) and elevated temperatures that seem to be tolerated by *A. montanus* larval stages (Dunham *et al.* 2007) suggest that the developmental trajectory of pre-hatching stages may also differ from that of *A. truei*.

Larval (*Tadpole*) *Development*: As addressed here, larval development includes the interval from hatching to the initiation of metamorphosis.

Ascaphus truei: Scattered data exist for *A. truei* during early larval development. At hatching, an embryo becomes a larva (or tadpole) upon their head-first emergence from its egg capsule; muscular contractions of its large flat tail facilitate the process (Brown 1989). Hatchling *A. truei* have a large ventral yolk sac, a median adhesive organ (Brown 1975), and almost no pigmentation (Brown 1989), giving them an almost white appearance. When reared at a constant 11ºC,[134] young larvae did not attach to the sides of their culture bowl until they had a functional suctorial mouth with well-developed labial teeth and branchial chambers; this occurred 38 days (5.4 weeks) after hatching. Over the 59-day interval after hatching, Brown (1975) found that larvae reared at a constant 11ºC increased from 11.0 to 20.1 mm total length and from 6.0 to 13.1 mm tail length. The increase in tail length (2.2-fold) was greater than the increase in total length (1.8-fold), indicating that greater allocation devoted to lengthening the muscular tail, presumably critical to larval survival in flowing water.

Adams (1993) collected 33 newly hatched larvae under or near the boulder where he found an egg mass (described previously) with 27 eggs in broken strings. Among these larvae were several that had hatched as Adams collected them. Twenty-three of these had a total length averaging 11.5 mm (10.5-12.1 mm).[135] The smallest approximated the developmental stage of newly hatched larvae described by Brown (1989), though the adhesive organ may have been slightly more developed. Based on comparison with older larvae, newly hatched larvae lacked directed swimming ability and developed oral disks. The latter would prevent them from clinging to rock surfaces and the former could prevent them from finding suitable low-flow habitat. Hence, barring disturbance, recently hatched larvae may typically locate in sheltered (interstitial) habitat.

Karraker and Beyersdorf (1997) observed eight newly hatched larvae on 26 August in the pool immediately below an oviposition site found on 16 August where eight unhatched viable eggs remained. On 2 September, they returned to the site and

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[134] A temperature in the midrange of summer temperatures recorded for *Ascaphus* streams in Washington State.

[135] These measurements were obtained after preservation.

recorded 23 recently hatched larvae; no unhatched eggs remained. The first larval descriptions they provided for individuals from this clutch were not until 20 September, when many larvae would have been about a month post-hatching. At that time, larvae already looked similar to older larvae; they had functioning oral disks (three were attached to rocks) and were dark gray in color with the characteristic white tail spot.[136]

Until *A. truei* larvae fully develop their swimming ability and mouthparts, they likely remain at or near their oviposition site, as observation of larvae prior to this stage are almost invariably aggregations of more than a few individuals (Adams 1993, Karraker and Beyersdor 1997; M. Hayes, *unpublished data*). This behavior results in their being much less detectable than older larvae, as reflected by methods that sample nearer the surface (light-touch) versus deeper in the substrate (rubble-rousing; Quinn *et al.* 2007).

Adams (1993) believed that his discovery of recently hatched larvae in late summer contradicted Metter's (1964a) suggestion that young larvae overwinter at the oviposition site. Assuming that Metter meant to include some populations we now regard as *A. truei*,[137] no contradiction may exist if development occurs at lower temperatures. If development under the constant lower-temperature laboratory-rearing regimes of Brown (1975) approximates field conditions at higher elevations or latitudes, young larvae may be forced to overwinter at oviposition sites. This highlights the need to study variation in early development as a function of elevation and latitude.

Regardless of precise chronology, we term larvae with well-developed mouthparts and darker coloration older larvae. Larvae become free-swimming with well-developed mouthparts coincident with their taking on the typical darker coloration, which occurs from late August to early September at lower elevations (Adams 1993, Karraker and Beyersdorf 1997). Older larvae, which had been discovered as early as 1911, were not recognized as belonging to *A. truei* until after Gaige (1920) described them. She described what we term older larvae here as “most curious” in both habits and appearance. Referring to their coloration, Gaige noted that these larvae superficially resemble the larger larvae of toads,[138] either all black or blackish brown thickly speckled with black, with all black eyes, and lacking iridescence. She described their tails as all dark like the body, or obscurely or strongly spotted with creamy white, noting that the tip may be creamy white with a dark band just behind it. She added that such larvae may sometimes have light spotting, which may occasionally be rose- or flame-colored. Gaige felt that the rose or flame coloration made them conspicuous.

Gaige (1920) also emphasized four morphological features of older *A. truei* larvae as distinctive when compared to the older larvae of all other anurans.[139] These included:

1) an unusually long tail, the muscular portion of which is so broad that the fins, which are heavily pigmented, are inconspicuous;

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[136] Though the white tail spot was described as characteristic in this description, its presence is highly variable among *A. truei* larvae.

[137] The work of Metter (1964a) encompassed populations included under each of what is now *A. truei* and *A. montanus*.

[138] Gaige (1920) did not specify what toad species was intended in this comparison, but the western toad (*Anaxyrus* [formerly *Bufo*] *boreas*) is presumed.

[139] Except for *Rana boylii*, all other North American anurans that have denticles around the mouth and beaks on their mandibles (a few [e.g. microhylid frogs] lack both) have 2-5 fewer tooth rows on the lower mandible and beaks on both mandibles. *Rana boylii* can have as many as 7 tooth rows on the lower mandible, but has a well-developed dark-colored beak on each mandible (Zweifel 1955).

2) unique mouthparts associated with a greatly expanded, ventrally oriented sucking type oral disk, which include an unusually high number of denticle (tooth) rows (2-3 rows above [or anterior] to the mouth and 7-10 rows below [or posterior to the mouth]); a white-edged horny black beak on the upper mandible; and a beakless lower mandible.
3) a spiracle[140] inconspicuously centrally located either just behind or concealed beneath the lower lip.
4) The anal opening is concealed under the tip of a prominent flap that is attached to the body at its base and to the tail by a thin membrane.[141]

Gaige (1920) also provided initial data on the behavior of older larvae. In particular, she emphasized use of their suctorial mouthparts to cling to instream rocks, to which they could sometimes attach so firmly that they were difficult to dislodge. She further noted that one could find them in cascades or waterfalls. She also found that it was possible to pick them up while they clung to a rock, or with care, induce them to attach to a finger. Gaige recorded older larvae in fast water and quieter pools, either concealed or surface visible, invariably with their tails directed downstream. She also noted that when disturbed, older larvae invariably swam upstream.[142] When detaching in flowing water that could carry them downstream, they quickly reattached. Gaige concluded that older larvae make few movements when undisturbed, occasionally wriggling over the surface of their attachment rocks.

Myers (1931) made a few observations on the ecology and morphology of older larvae in the Coast Redwood region of northwestern California that largely agree with those of Gaige (1920). However, he added that finding older larvae in the swifter portions of a small brook suggested a preference for riffles despite the fact that both these and the slower-flowing algal-dominated sections were rocky. He also commented that casual examination could miss larvae due to their preference for riffles, though their dark color and milk-white tail tip increases their visibility on rock surfaces.

Some data indicate distinct diel variation in the behavior of older larvae. In an experimental laboratory stream 30 cm wide × 10 cm deep × 2 m long with an electric paddle wheel-maintained 30 cm/sec flow velocity, Altig and Brodie (1972) found that 28-35 mm total length older *A. truei* larvae[143] moved to the upper surfaces of rocks at dusk and remained there all night; some were also active on cloudy afternoons. Their comment seems to imply that older larvae conceal themselves more frequently beneath rocks during the day. Hawkins and colleagues (1988) found significant differences in substrate use between day and night. At night, most larvae (42%) were collected from the largest substrates (>30 cm in dia) compared with only 25% during daylight hours. Larger substrates may be more suitable for grazing. Observations also suggest that the

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[140] The spiracle is the structure in anuran larvae through which water taken in through either the nares (nostrils) or the mouth exits the body; in the case of tailed frogs, because they are usually attached to rocks, the water is taken in is through the nares (Altig and Brodie 1972). Larvae of all other North American anurans have the spiracle located on the right or left sides of the body.

[141] Among larvae of other anurans with which tailed frogs co-occur in the Pacific Northwest, the anal opening is located on the left or right sides of the flap at the base of the tail.

[142] Though swimming upstream following disturbance is the typical pattern for older larvae, the statement of Gaige (1920) does not correctly characterize the range of responses. Older larvae will sometimes swim downstream after they have been disturbed.

[143] Older larvae that Altig and Brodie (1972) used in their experimental stream were collected from Mary's Peak, Benton County, Oregon.

diel pattern of concealment is highly variable among streams on the west slope of the Cascade Mountains in Washington State (L. Jones, *pers. comm.*).

Older larvae also exhibit rather stereotypical behaviors. In the experimental stream described above and in the field, Altig and Brodie (1972) noted that older larvae often occupy locations near the tops of rocks, a behavior that protects them from the full force of current and is located near preferred food, or both. They further described older larvae as lethargic, and allow themselves to be scooted over the substrate when initial contact with them is gentle. In agreement with Gaige (1920), they thought that older larvae seldom swam, but the frequency with which older larvae swim is unquantified. In the experimental stream, Altig and Brodie (1972) also found older larvae to exhibit strong positive rheotaxis (face into the current) and negative phototaxis (avoid strong light), patterns that agree with some field observations (e.g., Gaige 1920, Myers 1931). However, Altig and Brodie (1972) also suggested that position maintenance and the rheotactic response seemed stronger than the photactic responses. Hawkins and colleagues (1988) added that negative phototaxis seems to affect only diel activity patterns, that is, larvae alter surface-active behaviors depending on light levels. High densities of older larvae in reaches with open canopies suggest that phototactic behavior alone is not a strong influence on distribution of larvae at the watershed-level.

Hawkins and colleagues (1988) estimated densities of *A. truei* larvae in streams disturbed in the 18 May 1980 eruption of Mt. St. Helens[144] over three years (1985-1987). Their intent was to quantify microhabitat use of two larval age classes and provide insight into the effect of watershed disturbance on larvae. In their two-year study, they found significant differences in larvae densities among three basin-scale disturbance classes.[145] Deforested sites had the lowest densities, streams where only the headwaters were forested had the highest densities, and streams with relatively intact forest had intermediate densities. Low densities at deforested sites appeared related to extensive embeddedness[146] within streams, whereas the highest densities in streams with forested headwaters versus those with relatively intact forests appeared related to greater instream productivity (see also Hawkins *et al.* 1983) and low embeddedness. Hawkins and colleagues (1988) also noted that their correlations between larval density and water temperature did not support an interpretation that low densities in deforested sites were due to high temperatures.[147] However, they measured water temperatures only in the lower reaches of each watershed, which may strongly affect the relationship. Moreover, Hawkins and colleagues (1988) found that larvae were almost invariably

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[144] Hawkins and colleagues (1988) sampled 8-13 small streams near Mt. St. Helens during 1985-1987. Streams were similar in drainage area (5-10 km^2) and gradient (15-20% slope), but their study basins differed in extent of disturbance caused by the 1980 eruption. Six watersheds had no forest because the entire forest blew down and all vegetation was killed; three other watersheds had only forest in their headwaters because the forests in the lower basins were destroyed, but trees in the upper basins (30-50% of the total basin area) were not killed; and vegetation and streams in the four remaining basins received heavy ash fall, but vegetation was not destroyed.

[145] In 1985 and 1986, sampling that occurred between late June and late August detected two older larvae size (age) classes, whereas in 1986, sampling occurred in September, which detected only one size class presumably because older second-year larvae had already metamorphosed.

[146] Embeddedness is a conceptually simple but application complicated parameter that describes the degree to which fine substrates (typically sand or finer) fill the interstitial matrices of coarse substrates (gravel or larger).

[147] Hawkins and colleagues (1988) found that water temperature, the only measured physical factor that varied substantially among sites, was not correlated with larval density ($r^2 = -0.05$ and -0.18 for mean and maximum temperature, respectively, across the 13 sites).

aggregated,[148] a pattern linked to the non-random distribution of microhabitats with respect to water velocity, embeddedness, and substrate size. In particular, mean densities were highest at intermediate current velocities (61 and 80 cm/sec), relatively low embeddedness values (21-40%), and relatively coarser inorganic substrate sizes (10-30 cm in dia). In a laboratory test where older larvae were given a substrate size choice, Altig and Brodie (1972) found that smooth rocks ≥55 mm in diameter were preferred. Altig and Brodie (1972) used only the larger larval size class in their experiments, whereas Hawkins and colleagues (1988) averaged their result from two larval age classes (both the smaller and larger larval size classes in a region with a two-year larval cycle).

Substantial variation exists in detectability of older *A. truei* larvae, which depends both on their basic behavior, as described above, season and predators. Feminella and Hawkins (1994) reported that in the absence of predators,[149] larval activity was highest at night. Peak activity (>40% of larvae visible) occurred at 2200 hours and gradually declined thereafter with minimum activity (<5% of larvae visible) occurring from 0430 to 1620 hours. During daylight hours, larvae were almost always hidden from view beneath cobbles; only rarely would even the tips of their tails be visible at this time. Feminella and Hawkins (1994) also found that the number of *A. truei* larvae emerging from the cobble bed at night depended greatly on the predator species to which they were exposed.[150] Exposure to Coastal Giant Salamanders (*Dicamptodon tenebrosus*) resulted in a two-to-three fold reduction in activity when compared to larvae in predator-free controls. Reductions in activity (magnitude in parentheses) were also seen when larvae were exposed to either Cutthroat Trout (three-fold) or Brook Trout (six-fold), but not Shorthead Sculpin (*Cottus confusus*; no difference).[151] Variation also exists in the seasonal detectability of older larvae over *A. truei* geographic range. Based

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[148] Hawkins and colleagues (1988) noted that the only exceptions were for sites with overall low larval densities, for which dispersion patterns were apparently random. However, they also noted the low numbers in those cases limited both the statistical power.

[149] To quantify diel periodicity of *A. truei* larvae with or without non-visual cues from predators, Feminella and Hawkins (1994) used instream enclosures that were paired longitudinally (end-to-end). Enclosures were constructed of 103-cm long × 32.5-cm dia PVC pipe cut lengthwise and fitted with 6.4-mm mesh hardware-cloth ends and covers to allow water circulation, prevent larval escape, and exclude undesired predator entry. Periphyton-laden cobbles placed in the enclosures provided refuges and food for larvae (periphyton), and ballast (stability). Average water depth and current velocity in enclosures was 12 cm and 12 cm/s, respectively. Enclosures were established in a single uniform riffle about 10 m wide × 30 m long in the mainstem of Clearwater Creek. Before each experiment, the entire riffle with the enclosures and the adjacent upstream pool was electroshocked and seined to remove all predators whose presence might confound responses to experimental manipulations of predators. Counts of larvae that were partly or completely visible, later converted to percentages of the total number in each enclosure, were used to assess activity.

[150] Feminella and Hawkins (1994) used their enclosures (footnote 149) to conduct a series of separate 24-hour experiments in which they examined larval response to the presence of Brook Trout (*Salvelinus fontinalis*) and Cutthroat Trout (*Oncorhynchus clarkii*) (~200 mm total length), Shorthead Sculpins (80 mm total length), and Coastal Giant Salamanders (-160 mm total length). For each experiment, 15 *A. truei* larvae (25-30 mm total length) were placed in each of the downstream portion of the six enclosure pairs; and one individual of each predator species was confined in each of the upstream portion of three of the six enclosure pairs; the upstream portion of the remaining three enclosures served as controls.

[151] Though presence of shorthead sculpins at a density of one fish per enclosure resulted in no significant reduction in tadpole activity, researchers were concerned that the lack of larval response might have resulted from a potentially low dose of predator odor associated with the small body mass of the sculpins. As a consequence, Feminella and Hawkins (1994) conducted two follow-up experiments with densities of 2 and 5 sculpins per enclosure immediately after main experiment. The design in these experiments was identical except that more sculpins were used. Despite the increased densities, no significant differences in the activity of the predator-exposed treatment were observed.

on data from coastal western Washington, older larvae can be found year-around as long as air temperatures are at least 5°C (41°F; M. Hayes, *unpublished data*). In much of British Columbia, older larvae can be consistently found from May to October, though the highest numbers are generally encountered in July (Dupuis and Friele 1996; Wahbe 1996). Low numbers in spring and fall imply that larvae hide in substrate interstices. Though not statistically significant, Kroll and colleagues (2008) noted a declining trend in detectability of *A. truei*, represented by mostly larvae, as the summer season advanced. In general, older larvae are detectable for longer periods of time as elevation and latitude decrease.

Few data exist on reach-scale movements of older *A. truei* larvae. In a reach-scale study conducted in British Columbia in 1995-1996, Wahbe and Bunnell (2001) examined three replicates in each of three Western Hemlock (*Tsuga heterophylla*) forest types: unmanaged old growth (250+ years old), mature second growth (60-80 years since the last harvest), and recent clearcut (~5 years since harvest). Each replicate, located in a separate stream,[152] had three 5-m reaches spaced at 25-m intervals.[153] Larvae were reach-unique marked with initial surveys conducted in June or early July[154] and resurveys in July and August (each survey ~20 days apart).[155] Foci of the study were the relationship between larval movement and each of forest management, logjams, and gradient. Logjams, visually assessed, were scored on a qualitative scale.[156] Based on this scoring, old-growth ($\bar{x} = 1.7 \pm 0.33$ SE) had fewer logjams than either mature second-growth (2.7 ± 0.17) or clearcuts (2.8 ± 0.17). Wahbe and Bunnell (2001) also found that daily larval movement distances (m/dy) were greater in old-growth (1.10 ± 0.17) than either of second-growth (0.28 ± 0.10) or clearcuts (0.15 ± 0.12).[157] They interpreted this pattern to reflect logjam impediment to larvae movement, but their regression, albeit significant, resulted in logjams explaining only 13 percent of the variation in movement rates. Further, their sampling approach was not designed to address detectability, which could decline with more complex habitat (more logjams). Wahbe and Bunnell (2001) found no relationship between stream gradient and daily movement distances, but showed significant downstream movement among older *A. truei* larvae, a pattern they interpret to reflect larval drift (Müller 1974). However, they had very low recapture rates (7%) so how important downstream movement is to the larval population as a whole is unclear. This result appears to conflict with upstream movement of larvae recorded over much of the same season in southwest Washington

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[152] Replicate study sites were distributed on separate tributaries within 4 stream basins that flow into Howe Sound (the Ashlu, Elaho, Mamquam, and Squamish Rivers). In 1996, the Squamish clearcut site was replaced by the Ashlu clearcut site due to loss of road access. Streams were selected on the basis of the presence of *A. truei* larvae and except for the Ashlu and Mamquam clearcut site, were located upstream from logging roads.

[153] Placement of the downstream-most reach was random.

[154] Surveys consisted of area-constrained searches performed by initially scanning the stream for surface-active larvae, then slowing moving upstream and turning and brushing the undersides of rocks and capturing larvae with dipnets as they were dislodged (Wahbe and Bunnell 2001). Searches were conducted between 0700 and 2200 hr, and took three surveyors an average of three hours per stream for the actual larvae sampling with an additional three hours to process larvae and record stream parameters.

[155] To maximize recaptures, an additional 10-m reach was surveyed immediately below each of the middle and upper 5-m reaches in each replicate on each resurvey date. No 10-m reach was added below the downstream-most 5-m reach because a distance of 50 m had to be maintained from logging roads or the margin of clearcut units.

[156] Low (1), medium (2), or high (3) based on stream log densities, and the degree to which logs were imbedded in the stream.

[157] Duncan's multiple range test: $P < 0.05$.

(Hayes *et al*. 2006). However, Hayes and colleagues' results were not based on recapture of marked animals and can be explained by the possibility that individuals in the downstream portion of study streams are metamorphosing before individuals in the upstream portion of the same streams. Larvae may also be moving in response to stream drying (Hunter *et al*. 2005, Hayes *et al*. 2006).

Length of larval life in *A. truei* varies greatly with latitude and elevation. The basis of this variation is a function of growing season length that is influenced by aspect, gradient, snowpack and frost-free days (Dupuis 1999). This results in a larval life ranging from 1-4 years (or 2-5 different seasons)[158] depending on location (Ricker and Logier 1935; Metter 1964*a*, 1967; Brown 1990; Bury and Corn 1991; Gray 1992; Wahbe 1996; Wallace and Diller 1998; Bury and Adams 1999). Depending on coastal versus inland position and elevation, larvae from streams in northern California and southern Oregon have a 1- or 2-year larval period (Wallace and Diller 1998; Bury and Adams 1999; R. Bury, *unpublished data*). Populations below mid-elevations in Oregon, Washington, and British Columbia have a 2-year larval period, whereas many Cascade Mountain populations and all those studied on the east Cascade slope appear to have a 3-year larval period (Ricker and Logier 1935, Metter 1967; Kelsey 1995; Bury and Adams 1999). Several northern populations (northern Cascade Mountains and British Columbia) have larval size-frequency patterns that suggest a 3- to 4-year larval life (Brown 1990; Wahbe 1996). All studies examining the influence of elevation show that higher elevation sites have longer larval periods than nearby lower-elevation sites (Wallace and Diller 1998 and sources cited therein).

Older *A. truei* larvae are largely grazers. Tadpoles appear to consume mostly diatoms (non-filamentous algae), but this may simply be a bias that reflects the recognizability of the frustules of diatoms, their highly ornamented siliceous cell walls (Round and Crawford 1990). Some authors report that small amounts of filamentous algae and desmids are eaten (Metter 1964*a*; see also Franz [1970a] for *A. montanus*), but no systematic assessment of larval diet has ever been untaken through extensive grazing on bacteria-dominated biofilms is suspected (J. Richardson, *pers. comm*.). If diatoms are actually preferred, that preference may be based on their relatively high nutritional value. Selected diatoms may have a higher protein content than other algal taxa. Larvae of the only other stream-adapted anuran in North America, the Foothill Yellow-legged Frog, *Rana boylii*, also seem to prefer diatoms (Kupferberg 1997). During the spring, large amounts of pollen have also been found in the intestines of larvae (Metter 1964*a*). Foraging opportunities for larvae are likely highest during the summer months when productivity of algae is at its peak. During this time, larvae store fat for the coming winter. Forested streams of the PNW are often light-limited by forest canopies or topography. As greater sunlight reaches the stream, primary production increases, changing the composition and amounts of periphyton (Hawkins *et al.* 1983). In an artificial channel experiment manipulating stream nutrient supply and larval density, Kiffney and Richardson (2001) found that both growth rates and final biomass of *A. truei* larvae were significantly greater in nutrient-enriched treatment streams than in controls. They suggest that *A. truei* may frequently be resource-limited in headwater

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[158] For a 1-year larval life, individuals hatched in one season (the year they are laid as eggs) will overwinter and metamorphose the following season. Hence, the number of seasons spent as a larva always equals one more than the actual interval in number of chronological years.

streams and both develop faster and undergo metamorphosis earlier in productive streams compared with unproductive ones (Kiffney and Richardson 2001). Precisely how such a pattern may play out across the range of *A. truei* is poorly understood, but resource limitation might be expected to be more frequent at higher latitudes, and in forests with denser canopies, such as coastal forests.

Older *A. truei* larvae graze distinctively. Altig and Brodie (1972) showed that removal of material from rock surfaces was the primary mode of feeding. The upper jaw being large, plate-like (FIGURE 5), lying parallel to the substrate and non-occlusive to a reduced low jaw,[159] and the mouth simultaneously have to serve as an attachment organ make the mechanics of removing material from rock surfaces complex. Older larvae engage in shuffling or sliding feeding action so the lower jaw, alone in or conjunction with the labial denticles, loosen material from rocks. However, as Gradwell (1971, 1973) observed, the upper jaw can turn enough during a slide or shuffle to scrape the substrate. In combination with the labial denticles, the action of the upper jaw also functions in the hitching locomotion of older larvae. Older larvae observed in non-flowing water with suspended organic particles[160] revealed currents entering the nares and no evidence of leakage around the oral disc (Altig and Brodie 1972). Though fewer particles entered than exited the spiracle, filtering particles through the nares was not considered an important feeding mode.

Knowledge of predators on *A. truei* larvae is limited. Morrissey and Olenick (2004) observed American Dipper (*Cinclus americanus*) adults feeding older *A. truei* larvae to their young at a nest. Nussbaum and colleagues (1983) commented that Cope's Giant Salamanders eat larval *A. truei* without further details. Cope's giant salamander and *A. truei* larvae are frequently syntopic in the Olympic, Willapa Hills, and South Cascades physiographic regions of Washington (Adams and Bury 2000, 2002; M. Hayes, *unpublished data*), so this typically neotenic species may be a focal predator on larvae. Schonberger (1945) reported a Common Garter Snake (*Thamnophis sirtalis*) from near Lake Cushman (Washington) eating an *A. truei*, but specified no life stage. Coastal Giant Salamanders and Cutthroat Trout are suspected predators (see Metter 1963 and Daugherty and Sheldon 1982b for *A. montanus*), but this relationship has never been reported. Larvae show behavioral avoidance responses to water conditioned by Brook Trout and Shorthead Sculpins, indicating they are potential predators (Feminella and Hawkins 1994), but actual predation events by these taxa remain undocumented. The avoidance response to Brook Trout is curious given that it is an introduced species throughout the geographic range of *A. truei*; hence, this avoidance behavior may reflect a generalized co-evolved response to salmonid predators, rather than a species-specific response to Brook Trout. Altig and Channing (1993) hypothesized that aerial attacks on *A. truei* larvae focused on the tail rather than the cryptically colored body. They based this conjecture on the presence of a white spot at the tail tip and Caldwell's (1982) original suggestion that differentially pigmented tails among anuran larvae had the purpose of orienting predators away from the head. Blair and Wassersug (2000) confirmed this notion based on finding a marked concentration of predator-attributable damage around the tail tip on 81 older *A. truei* larvae from central Oregon. The area

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[159] The small non-keratinized lower jaw differs from the rather large expanded oral disk with 7-10 denticle (tooth) rows that is attached to it.

[160] Observations were made at 30× magnification (Altig and Brodie 1972).

found most frequently damaged in *A. truei* larvae bore a remarkable resemblance to the shape of the white spot at the tip of its tail. As a corollary to this idea, Wahbe (1996) observed vertical wagging of tail fins, which she believed provided a visual stimulus to potential predators. Additionally, Blair and Wassersug (2000) found that the amount of tail damage increased with age. The positive relationship between developmental stage and percent damage in older *A. truei* larvae suggests that the color spot attract predators and that the longer the tadpoles are in the stream the more predatory strikes their tail tips sustain (Blair and Wassersug 2000). Altig and Channing (1993) also hypothesized that the location of the tail spot would result in aquatic predators typically attacking *A. truei* larvae from behind, but this hypothesis remains untested. Dupuis (1999) noted that north of the Fraser River in British Columbia, where Coastal Giant Salamanders are not known to occur; *A. truei* larvae are diurnal and nocturnal, implying that giant salamander presence represents a predation risk that influences larvae diel activity. This hypothesis may be confounded to some degree with a thermally driven need to be more diurnal at higher latitudes notwithstanding other influences.

Ascaphus montanus: Information on larvae and larval development is more limited for *A. montanus* than for *A. truei*. Based on few data, *A. montanus* hatch in late summer. Based on descriptions from the Palouse and Touchet sites of Metter (1964a), hatching would have occurred in late August-early September. In northwestern Montana, hatching of the translocated eggs presumably laid in mid-July occurred in the 3-5 September interval (Franz 1970*a*).

At his Palouse and Touchet sites, Metter (1964a) described hatching larvae as white and 13-15 mm TL. He noted that the pigmentation characteristic of older larvae is not acquired until the animals are about 18 mm long, though the beak is still not fully formed and the yolk not fully absorbed until the larvae reach 20-21 mm TL. Dissected young larvae had only yolk in their digestive tracts. Metter (1964a) thought that young larvae[161] do not leave the oviposition site until the yolk is completely used in winter or early spring based on the fact that he found young larvae containing yolk aggregated under boulders. He interpreted these to be sib groups at oviposition sites. Moreover, he found such aggregations in August-September and in April-May of the next year. Based on development from eggs translocated from Twelve-Mile Creek to a similar creek near the Flathead Lake Biological Station (Franz 1970*a*),[162] hatchling *A. montanus* larvae had a large yolk sac and were near-white in color due to an overall fine sprinkling of melanin except on the distal fin; the area around the upper part of the eyes had the most melanin. Six larvae, measured at hatching, averaged 12.8 mm TL (± 0.3 mm SD). Early growth was rapid; two days later, three individuals that each were 13.0 mm TL upon emergence averaged 13.7 mm TL (± 0.4 mm SD).

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[161] Based on a small body size (≤18 mm), incomplete pigmentation, and significant unabsorbed yolk.

[162] See page 41 for details on the translocation circumstances and description.

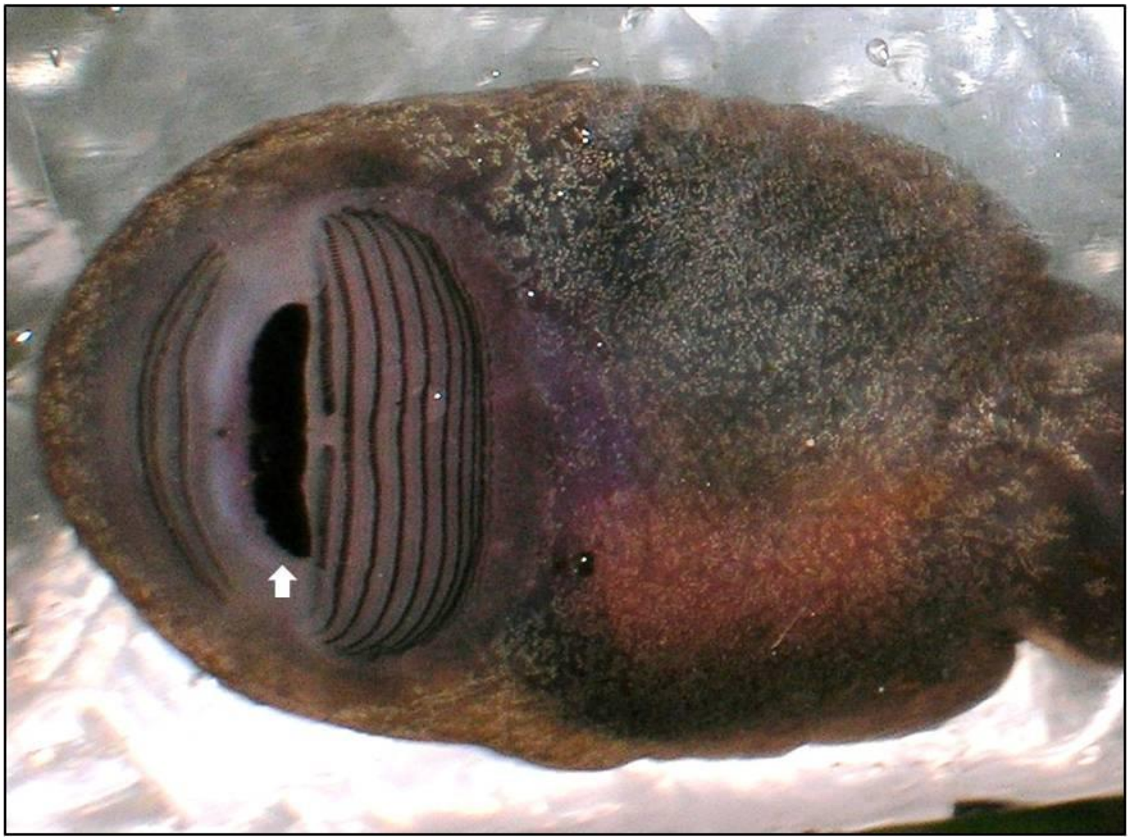

FIGURE 5. Close-up of *Ascaphus truei* larva (tadpole) mouthparts.

White arrow indicates the dark, plate-like upper jaw that has no counterpart on the lower jaw. (Photograph credit: Julie Tyson).

Relatively few data exist regarding various aspects of the behavior of older *A. montanus* larvae. Metter (1964a) observed older larvae climbing above the water surface on spray-drenched rocks only at night. He commented that several workers have speculated that older larvae do this to reach richer food, but thought this unlikely based on their diatom-focused diet. Alternative reasons were not offered, but the behavior may be anti-predatory directed at avoiding larval Idaho Giant Salamanders (*Dicamptodon aterrimus*; see next paragraph) if the latter are most active at night.[163]

Working in Youngs Creek in northwestern Montana and Mica Creek in northern Idaho, Jones (2008) found that older larvae (2-3 year old) were patchier in their distribution, often aggregating under or on a single rock within the 5-m channel units he sampled. In contrast, 1st-year larvae were typically scattered. The focus of Jones' (2008) work was to compare the distribution and abundance of *A. montanus* larvae varied between the biogeoclimatically distinct Youngs and Mica Creeks. In each stream network, Jones (2008) distributed his sampling units from each creek's confluence with the larger river upstream through a subset of third, second, and first-order tributaries to their respective headwaters. Surveys were done with kick nets and snorkeling between late June and

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[163] Data on *D. aterrimus* activity are lacking, but difficulty in detecting them using standard diurnal light-touch surveys implies that nocturnal behavior may be typical (Sepulveda and Lowe 2009).

early August in 2005 and 2006, during the descending limb of the hydrograph.[164] Based on 4,471 captures in 485 sampling units distributed over 124 km (77 mi) of stream in the two networks, *A. montanus* larvae were broadly distributed across both creek systems. Notably, some larvae were present in the largest stream reaches; specifically, in reaches up to 13 m (43 ft) wide on Mica Creek and up to 18 m (59 ft) wide on Youngs Creek. In both streams, densities of 1st- and 3rd-year larvae decreased with increasing distance downstream, but the striking find of Jones (2008) was identifying the generally more upstream location of younger (1st-year) larvae and the relatively more downstream position of older (3rd-year) larvae in both systems (see his Figure 2). This pattern was clearly reflected in the more rapid decline in density of 1st-year larvae relative to 3rd-year larvae as one moved downstream. This pattern is basically opposite to the distribution of larval age classes that Hayes and colleagues (2006) reported for *A. truei*, where on average, older larvae were more frequent as one moved upstream, and may indicate yet another way in which the two species differ. Beyond this basic distribution pattern, Jones (2008) did find the densities distribution of larvae differed between the two stream networks. In Youngs Creek, a glacial and lake-fed stream, larvae peaked in density closer to the stream's origin, whereas in Mica Creek, a spring fed network, larval density peaked further downstream. Jones (2008) speculated that the difference in stream origins, potentially affecting the quality of headwater habitat for larvae, might explain the difference in larval distribution between the two creeks.

As with *A. truei*, knowledge of the predator set on *A. montanus* larvae is limited. Metter (1963) dissected 50 *D. aterrimus* (given as *D. ensatus*) in a diet study. He considered *A. montanus* larvae to be important prey for large *D. aterrimus* when they occupy the same stream; every *D. aterrimus* he examined over 95 mm SVL (n = 7) contained an *A. montanus* larva. Nonetheless, based on the numbers of *A. montanus* larvae present, Metter (1963) did not consider this predation to be a threat to the population in the headwaters of the Palouse River. At his Touchet site, Metter (1964a) also encountered a Wandering Gartersnake (*Thamnophis elegans vagrans*) eating an *A. montanus* larva. Further, he concluded that this snake species feeds extensively on *A. montanus* larvae based on finding mainly diatoms in the fecal material from the Wandering Gartersnakes on the Touchet. Daugherty and Sheldon (1982b) also observed garter snakes (*Thamnophis*, species unspecified) at their Montana study site, but predation was not reported. Cutthroat Trout and American Dippers, known predators of *A. truei*, co-occur with *A. montanus* (Daugherty and Sheldon 1982b), but predation by these species is as yet unreported. Other predators reported or suspected for *A. truei* (see page 59) may also prey on *A. montanus*.

Length of the larval period in *A. montanus* appears to vary less than in *A. truei*, which may reflect in part the more contracted geographic range of the latter. All four populations studied to date have a 3-year larval period, including the upper Palouse (Idaho; Metter 1964*a*, 1967), the upper Touchet (Washington; Metter 1964*a*, 1967), the upper Clark's Fork (Montana; Daugherty and Sheldon 1982a) and the upper Grande Ronde (Oregon; Bull and Carter 1996*a*). This conclusion is largely based on finding 3

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[164] Jones (2008) stratified stream segments by order and length, randomly placed a number of 250-m sample reaches proportional to the length of the segment, and placed five 1-5 m sampling units randomly placed within each sample reach. Based on a hypothesized tailed frog tadpole drift rate of 4 m/dy derived from the work of Wahbe and Bunnell (2001) on *A. truei*, he placed sample reaches 200-1000 m apart to ensure independence for analyses.

distinct larval size classes in streams during June-August (Metter 1964a, 1967; Daugherty and Sheldon 1982b, Bull and Carter 1996a, Jones 2008). Whether northern or higher elevation populations in the Rocky Mountains exhibit longer larval intervals as occurs in *A. truei* is unknown (Wallace and Diller 1998, Bury and Adams 1999).

Like *A. truei*, older larvae of *A. montanus* are grazers. Metter (1964a) examined the intestinal contents of five larvae from each of his Palouse and Touchet study sites in each month from April through October. Diatoms were the only major recognizable item found in all larvae. No significant differences existed between sites and the only seasonal change was the appearance of conifer pollen in large amounts during June. Filamentous algae, desmids, and tiny insect larvae were rare; however, the comments on potentially highly digestible biofilms made for *A. truei* likely also apply here. Thirty to 40 percent of gut contents was sand grains ingested incidentally. Based on data from northwestern Montana, Franz (1970b) also found the diet of older larvae to be diatom-dominated.[165] Scattered among the diatoms were the remains of small aquatic tendipedid (Chironomidae) midge larvae, a small amount of pine (*Pinus*) pollen (species unspecified), a few strands of the green alga *Ulothrix*, and bits of mineral matter. Though the green algae *Spirogyra* and *Monostroma* were abundant at one of the sites sampled, none were found in larval digestive tracts.

Metamorphosis: Metamorphosis (FIGURE 2), the period over which grazing larvae are transformed into carnivorous (primarily insectivorous) post-metamorphic juveniles, is short in comparison to the time required for other life stages. Metamorphosis is begins when the first forelimb erupts through the body wall and is complete when a four-limbed animal has completely reabsorbed its post-cloacal tail.

Ascaphus truei: Carl and Cowan (1945) provided preliminary laboratory-based data on the metamorphic interval. Based on one of two second-year larvae collected on 2 June 1942, this larva had four limbs but retained a suctorial mouth, albeit reduced in size, on 13 August 1942. By 2 September 1942, it had completely lost its suctorial mouth, but still had a post-cloacal tail. This individual was accidentally lost before it was able to complete metamorphosis after 2 September. As metamorphosis began some time before 13 August and would have ended sometime after 2 September, the entire metamorphic interval would extend more than 20 days. Metter (1964a) stated that Carl and Cowan (1945) indicated that 30 to 50 days were needed for their laboratory-housed larva to complete metamorphosis, but Carl and Cowan (1945) made no such statement. Brown (1990) commented that accelerated changes in morphology occur at the end of summer within a two to three week period, but whether his comment was meant to apply to the entire metamorphic interval is not clear. Discussing *A. truei* in coastal California, Oregon, and Washington, Bury and Adams (1999) commented that metamorphosis seems constrained to a relatively short period, but did not specify the meaning of short. Their observation of metamorphosis mostly during August might indicate a

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[165] Franz (1970b) obtained a series of 25 *A. montanus* larvae from each of two streams, Coyle and Ward Creeks (located, respectively 5.5 km [3.4 mi] and 11.2 km [7.0 mi] NW of St. Regis, Mineral County), both tributaries of the St. Regis River. Twelve animals from each series were preserved upon capture to arrest digestion for gut content examination. Franz (1970b) noted that the most interesting substance that was found in the digestive tracts of the preserved *A. montanus* larvae was a mass of golden brown "pigment" resembling the coloring bodies in diatoms. Several complete but empty diatom valves were associated with this pigment, leading him to believe that this mass was simply partly digested diatoms. Further, 13 larvae that were maintained alive from each group were places in clean containers and not fed supplemental food for a brief interval; all these produced diatom-dominated feces.

metamorphic interval within a month, but the coarse resolution of their data makes such a conclusion ambiguous.

Metamorphic timing appears to be late summer. The laboratory-housed animal on which Carl and Cowan (1945) reported would have metamorphosed in September. In his higher elevation population, Brown (1990) recorded metamorphosis in August and early September. Jones and Raphael (1998) observed metamorphosing individuals in August. Though Bury and Adams (1999) recorded most metamorphosis in August, some individuals metamorphosed as early as late June. Wahbe and Bunnell (2000) also reported late summer metamorphosis in British Columbia. A cline in the timing of metamorphosis is anticipated with both latitude and elevation, but existing data lack enough resolution or uniformity to evaluate that possibility. Metamorphic timing could also be strongly affected by water availability, but how drought versus wet years might affect that timing has not been examined.

Similar to other anurans, metamorphosing *Ascaphus truei* probably do not eat when their gut morphology is being reorganized. All metamorphosing *A. montanus* Metter (1964a) examined (number unspecified) had empty digestive tracts, and *A. truei* is anticipated to behave similarly.

Jones and Raphael (1998) observed a hellgrammite and Cope’s Giant Salamander attacking, respectively, a 17 mm and a 19 mm SVL metamorphosing *A. truei* on the Olympic Peninsula. They suggested that *A. truei* late in the metamorphic process may be more conspicuous and hence susceptible to predators than either larvae or post-metamorphic juveniles and adults. Such vulnerability would be expected given that many anuran species have been documented to be more vulnerable to predation during metamorphosis than other life stages (e.g., Wassersug and Sperry 1977, Arnold and Wassersug 1978).

Movement of metamorphosing *A. truei* is unstudied. However, Wahbe and colleagues (2004) described most of their juveniles as having a residual tail, which represents individuals nearing the end of metamorphosis. If this is the case, *A. truei* nearing the end of metamorphosis may engage in fall movements similar to juveniles; see section on juvenile *A. truei* for details.

Ascaphus montanus: Data obtained during the metamorphic interval for *A. montanus* are sparse. Based on animals from his Palouse and Touchet sites, Metter (1964a) commented that transformation required about 60 days but did not elaborate. Similar to *A. truei*, metamorphosis is recorded as occurring in late summer. Metter (1964a) found that the front legs first erupted around the first of July but the tail was not resorbed until late August or early September. At Butler Creek in Montana, Daugherty and Sheldon (1982a) did not specify when metamorphosis typically began each year, but they indicated that metamorphosis was usually completed during September. However, they added that occasionally an individual at the end of metamorphosis, as evidenced by a remnant larval tail, was observed the following spring. Based on data from the Wallowa Mountains of Oregon in 1992, Bull and Carter (1996a) encountered a similar pattern, with metamorphosing frogs found from July to September. The percentage of metamorphosing frogs captured in July that were still resorbing tails was 100% (n = 3); 68% in August (n = 38); and 22% in September (n = 6). Metamorphosing animals did not appear to eat (Metter 1964a); all individuals examined had empty digestive tracts.

Juvenile Development: Juvenile development is the period over which a metamorphosed (transformed) juvenile develops into a mature adult.

Ascaphus truei: Few data exist on the length of time *A. truei* are juveniles. Based on nocturnal surveys in 6 streams in northwestern coastal California over the interval 2002-2004,[166] males and females spent 1.5-2 and 2.5-3 years, respectively, as juveniles (Burkholder and Diller 2007). These are the only data on juvenile lifespan for *A. truei* and they come from the southern end of the range where the larval lifespan can be completed in one year (Wallace and Diller 1998, Bury and Adams 1999), so we anticipate juvenile lifespan to vary with elevation, latitude, and other parameters.

Few data exist on the size of juvenile *A. truei*. In northwestern California, Burkholder and Diller (2007) found juvenile males ranged from 25 mm[167] just after metamorphosis to 33 mm just before sexual maturity. In contrast, juvenile females ranged from 26 mm after metamorphosis to 41 mm just prior to sexual maturity. In southwestern British Columbia, Wahbe and colleagues (2004) reported juveniles (not partitioned by sex) ranging from 16 mm to 28 mm. However, they described most of their juveniles as having a residual tail, which represents animals nearing the end of metamorphosis. Wahbe and colleagues (2004) also indicated that some of their adults lacked secondary sexual characteristics, so their adult category would have included some juveniles.

Van Winkle (1922) was the first to report post-metamorphic *A. truei* some distance from water,[168] but she did not specify whether juvenile, adults, or both life stages were involved. She implied that heavy rain the preceding night was responsible for *A. truei* being found far from the stream. The data of Bury and Corn (1987, 1988b) also suggest a rainfall-linked response; they found frog trap rates increased as rainfall increased during the fall.[169] One of the two dominant frog species trapped was *A. truei*, of which most had recently metamorphosed (Bury and Corn 1987). Furthermore, arrays were typically located >75 m (~250 ft) from forest edges, roads, or flowing water (Bury and Corn 1987, 1988b), which implies that juvenile *A. truei* is the dispersal life stage and that dispersal occurs during fall rains.

Wahbe and colleagues (2004) also used a pitfall trap grid to evaluate movement of *A. truei* in clear-cut versus old-growth forests of coastal southwestern British Columbia.

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[166] Burkholder and Diller (2007) conducted this study on streams located on Green Diamond Resource Company managed timberlands in Humboldt County, California. Study streams were second- or third-order located within the Coastal Redwood Zone and included five streams in Mad River drainage near Korbel (Bald Mountain, Lower Jiggs, Black Dog, Upper Jiggs, and Mule Creeks) and one in the Maple Creek drainage (North Fork Maple Creek). Except for Bald Mountain and Mule Creeks, streams were non-fish-bearing.

[167] This is body size measured as snout-to-vent length (SVL).

[168] Van Winkle (1922) stated, “The toads were taken among the fallen timber and underbrush, on the wooded mountain slope in an area of larch, hemlock and cedar trees. This is interesting to note, since all the specimens heretofore reported have been captured either in or near pools or under the rocks and along the banks of streams. Ours were not captured in water or at very close proximity to a stream. There had, however, been a very heavy rain the night before the day the toads were taken and the moss, brush and trees were wet.”

[169] Bury and Corn (1987) placed one pitfall trap array in 30 forested stands, 18 in the central Oregon and 12 in the southern Washington Cascades. Each array had 2 triads ~25 m apart. Each triad had 3 5-m-long drift fences that began 3 m from a center and radiated outwards at 120°. Trapping ran 180 days uninterrupted late May to late November 1983. Bury and Corn (1987) did not present individual species data, but they noted that most frog captures were recently metamorphosed *A. truei* and *R. aurora*. Fifty-nine (n = 663) and 27% (n = 252) of amphibians trapped in Washington and Oregon, respectively, were frogs; and frog trap rates significantly increased with increased rainfall (Spearman Rank correlation: $r_s = 0.52$, $P < 0.01$).

Trap arrays in this grid were placed 5, 25, 50, and 100 m from stream edges.[170] Of 146 juveniles captured over three years,[171] two-thirds were captured in the 5-m array. The rest were captured at the 25- (n = 27), 50- (n = 10), and 100-m (n = 11) distances. They also found that juveniles were captured closer to streams (17.2 m ± 4.5 m SD) than adults (28.9 m ± 6.7 m SD; $F_{1,210} = 2.3$; $P = 0.029$). Partitioning units between clear-cut and old growth, the same pattern was recorded in clear-cut units (juveniles: 14.4 m ± 3.1 m; adults: 37.3 m ± 7.2 m; $F_{1,4} = 8.5$, $P = 0.043$), but not in old-growth units (juveniles: 20.0 m ± 9.1 m; adults: 20.6 m ± 10.0 m; $F_{1,4} \leq 0.1$, $P = 0.969$). These differences led Wahbe and colleagues (2004) to conclude that juveniles remained closer to streams, particularly in clearcuts, likely due to a more advantageous microclimate. However, they also suggested that juvenile frogs perform more overland movements (and hence dispersal) than adults. To avoid the conclusion that these two statements are contradictory, one would need to assume that overland movements are largely restricted to the proximity of streams, which is difficult to understand. Wahbe and colleagues (2004) also recaptured 7% (n = 10) of their juveniles, over half of which had moved upstream. They speculated that movement upstream might compensate for downstream larval drift. In general, the interpretations and conclusions of Wahbe and colleagues (2004) should be regarded as starting points for further investigation.

In another study in southwestern British Columbia, Matsuda and Richardson (2005) used a different pitfall trap grid array to evaluate movements of post-metamorphic *A. truei*. Here, arrays[172] were placed 20 m from each other in a 4 × 4 grid approximately 5 m from and parallel to the stream axis. One grid was placed at each of six study sites. Body mass was used to group post-metamorphic frogs into three age classes, but only the smallest category could be unambiguously called juveniles.[173] Of the 175 post-metamorphic *A. truei* trapped, 66 percent were juveniles;[174] and another 21 post-metamorphic animals termed subadults could have included juveniles. In contrast to Wahbe and colleagues (2004), this study found no significant differences in capture frequencies between juveniles and other age groups with the distance from the stream. Further, based on pitfall capture location (see p. 65), most juveniles appeared to move parallel to the stream and this pattern was not significantly different from that of the

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[170] A grid of 48 pitfall traps was installed at each of six sites (3 along clear-cut harvested streams and 3 along old-growth streams). Each grid had four arrays with 12 traps each. Half the traps in the 25-, 50-, and 100-m arrays were located downslope of zig-zag drift fences paralleling the stream; remaining traps were located on their upslope side.

[171] Wahbe and colleagues (2004) trapped during two periods: summer (July–August) and fall (September–November). However, they trapped in summer only in 1999, an effort that yielded 13 frogs. During 3 years of fall trapping, Wahbe and colleagues (2004) captured most frogs (n = 241 for all three years combined) between 26 September and 23 October and no frogs in November, when snowfall occurred.

[172] Arrays consisted of an X-shaped drift fence with four 5-m arms and a pitfall trap placed in each elbow between two arms. Arrays were oriented such that the arms were at 45° angles to the stream axis so that traps in the elbows beginning with the one most proximate to the stream and moving clockwise in the upstream direction would face: toward the stream, upstream, away from the stream, and downstream. This design and placement was thought to allow researchers to the ability to judge movement direction (parentheses): facing stream (away from stream), facing upstream (moving downstream), facing away from stream (toward stream), and facing downstream (moving upstream).

[173] Frogs with a mass ≥4.00 g were considered adult (reproductive), those between 1.76 and 3.99 g were considered subadult (breeding capacity unknown), and those ≤1.75 g were considered immatures (pre-reproductive; Matsuda and Richardson 2005). Hence, only immatures were unambiguous juveniles.

[174] All individuals trapped were marked, but only first-time captures in pitfall traps were used in the analysis. The 175-individual sample consisted of exclusively first-time captures.

two older age classes. These data should be interpreted cautiously since this study had high inter-site variability and also suffered from low power.

In the most extensive study of post-metamorphic *A. truei* to date, Burkholder and Diller (2007) captured 2,146 post-metamorphic *A. truei* over 3 years (2002-2004).[175] Surveys, which were nocturnal to maximize captures, occurred 2-4 times a month during spring through fall, once per month in winter, and encompassed reaches 80-175 m long. Juvenile frogs seemed to display high site fidelity. Juveniles made relatively minimal movements, either up- or downstream. Most longitudinal movements (parallel to the stream axis) were 0-30 m and involved captures within the stream channel.[176] They also found no significant difference in the distribution of longitudinal movements between juvenile males and juvenile females. Recapture frequency was high (65% of all frogs [juveniles and adults] were recaptured), so a sense of population-level movements was obtained. Nonetheless, the relatively short length of sample reaches would have biased against capturing juveniles making long moves, but evaluating this possibility would require sampling a substantially larger area.

Few data exist on the growth of juvenile *A. truei*. Burkholder and Diller (2007) noted that *A. truei* grew year-round in northwestern California. They reported growth rates that included combined juveniles and adults, but their growth curves suggest that juveniles grow faster than adults. Collective growth rates were about 1.6 times as fast in summer (1.4-1.5 ± 0.1 mm/month, *n* = 143) as they were in winter (0.9 ± 0.04 mm/month, *n* = 7), and growth rates of females did not differ significantly from those of males.

Ascaphus montanus: The only data available for growth of *A. montanus* were collected by Daugherty and Sheldon (1982b), who demonstrated that *A. montanus* males from Butler Creek (Montana) remain juveniles for 4 years, where females are juveniles for 5 years. Juvenile lifespan for *A. montanus* is likely to vary with elevation, latitude, and perhaps other parameters.

Few data exist on movement of juvenile *A. montanus*. Daugherty and Sheldon (1982a) recorded 113 recaptures of juvenile *A. truei* (69 within-year recaptures and 44 between-year recaptures).[177] Of the only 10 juveniles recaptured that represented the recently metamorphosed cohort in any one year, only one was recaptured beyond 20-m of the original capture point, and that individual was caught in the immediately adjacent 20-m interval. Though older juveniles were sometimes recaptured as somewhat greater

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[175] Burkholder and Diller (2007) selected four streams to survey for post-metamorphic *A. truei* from a population of 17 streams chosen in a randomly stratified way to capture variation in geology, forest type, and amount of recent timber harvest. These 17 streams were also used for annual surveys of larvae.

[176] Logistics and safety limited stream access for night surveys to the same starting location. Given potential bias in observations of movements, Burkholder and Diller (2007) used only the absolute value of the longitudinal distance moved from the first capture location for analysis. No significant differences existed between longitudinal movements for frogs captured in multiple years compared to frogs recaptured within a year, so streams were pooled and only frogs that were recaptured at least three times were included in the analysis. All movements were considered independent because distances moved between captures were spaced by at least one to two weeks, and in most cases, several months existed between captures.

[177] Daugherty and Sheldon (1982a) assessed movement patterns in part from data obtained during a mark-recapture effort conducted over an 80-m long study reach that was divided into four 20-m segments and sampled 20-30 times each summer over five consecutive years (1973-1977). To assess potential long-distance movements, Daugherty and Sheldon (1982a) searched a reach from 800 m upstream from the 80-m mark-recapture reach to 2000 m downstream from that reach over 15 nights during each of two summers (1975-1976).

distances, these represented only 12% (n = 12) of the recaptures of older juveniles.[178] The maximum movement distance that Daugherty and Sheldon (1982a) recorded for any post-metamorphic life stage, which they interpreted as a dispersal movement, was 360 m move made by a juvenile female over a period of 12.5 months. The summer timing of Daugherty and Sheldon (1982a) assessment of movements may have missed the period when most longer moves occur (Adams and Frissell 2001). Some authors have speculated that newly metamorphosed individuals typically engage in upstream movement (Daugherty and Sheldon 1982a; Metter 1964*a*; but see also Wahbe *et al*. [2000] regarding juvenile *A. truei*). If larvae tend to drift downstream over the summer season, then upstream movement by juveniles could maintain the position of a local population in suitable habitat within a stream system (Müller 1974).

Few data also exist on the size of juvenile *A. montanus*. Based on work in the Wallowa Mountains of northeastern Oregon in 1992 and 1993, Bull and Carter (1996a) found juvenile *A. montanus* ranged from 28 to 35 mm SVL. They did not partition their juveniles by sex. Daugherty and Shelton (1982a) did not specify the size of the *A. montanus* they studied at sexual maturity, but based on their cohort data, the juvenile males would have ranged from ~20 to ~35 mm in total length (TL),[179] and juvenile females would have ranged from ~20 to ~46 mm TL.

Adulthood: Adulthood is the period between sexually maturity and death.

Ascaphus truei: Burkholder and Diller (2007) found that *A. truei* were active year-round in northwestern California, though activity was depressed in winter. In contrast, in British Columbia, *A. truei* was active from March to November (Maxcy 2000; Wahbe and Bunnell 2000). Judging levels of activity requires cautious interpretation because quiescence and immobility (see *The Overwintering Season* subsection) do not always characterize overwintering behavior. Regardless of the precise interpretation of activity, reduction in active-season length is anticipated with increasing latitude or elevation.

Adult *A. truei* may tolerate desiccation poorly. Adult *A. montanus* died after losing proportionally less mass than the 17 frog species with which they were compared (Claussen 1973b; see also Hillman *et al*. 2000 and pages 71-72 on *A. montanus* desiccation tolerance), so adult *A. truei* may respond in a similar way.

Nighttime activity typical of adult *A. truei* (e.g., Jones *et al*. 2005) may also be related to reducing water loss since higher humidity levels typically occur at night, especially in the absence of precipitation. On the other hand, eye morphology (vertical pupil) and a probable preference for a low level of illumination (see Hailman 1982 for *A. montanus*) suggests that nocturnal activity is intrinsic tailed frog behavior, though plasticity in their diel behavior is known. Metter (1967) found adults to be almost exclusively nocturnal in all his *A. truei* study sites except at Stevens Pass,[180] his highest

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[178] All these individuals were recaptured 50-70 m from their original capture locations.

[179] The body length measurement used by Daugherty and Sheldon (1982a) was total length rather than snout-to-vent (SVL) length. Total length is from the tip of the snout to the tip of the cloacal tail, which becomes proportionately larger in males with increasing body size. Females also have a reduced cloacal appendage, but it does not vary in size with ontogeny like the cloacal tail of males. As a consequence, total length provides a greater differential as a body size measurement between males and females than does SVL.

[180] The creek discussed at Stevens Pass (1,226 m [4,022 ft]) lies just west of the crest of the Cascade Mountains on the Chelan County/King County boundary, Washington.

elevation population. On four separate visits, Metter found adults surface-active along the stream banks during the day. On three of these visits, it was overcast and raining, but on the fourth trip, which was on a warm clear day, about 75 surface-active adults were also seen. On a fifth visit, also on a clear day, Metter found adults only by turning over instream rocks. At his nine other study sites in Oregon and Washington, Metter (1967) rarely encountered adults surface-active during the day. However, in the Coast Range of British Columbia, *A. truei* are active both nocturnally and diurnally (L. Dupuis; T. Wahbe, *unpublished data*). Unrecognized clines may exist in the tendency for diurnal activity with some combination of increasing latitude and/or elevation, but the local variation that Metter (1967) encountered remains unexplained.

The apparent preference of adult *A. truei* for stream-side habitat may also relate to their hydration needs. A number of studies have demonstrated more mesic conditions, presumably more favorable for hydration, along riparian corridors (Gregory *et al*. 1991; Chen *et al*. 1999) than in adjacent uplands. Various authors have commented that adult *A. truei* are detected most frequently near streams (Gomez and Anthony 1996; Maxcy 2000; Matsuda 2000, Matsuda and Richardson 2001, 2005; Wahbe *et al*. 2000, 2004; Burkholder and Diller 2007). This interpretation is likely correct though most pitfall trapping studies were not conducted outside of 100 m of the stream (Maxcy 2000; Matsuda 2000, Matsuda and Richardson 2001, 2005; Wahbe *et al*. 2000, 2004). Using a rectangular array in which the long axis was parallel to the stream at 15 western Oregon sites,[181] Gomez and Anthony (1996) captured *A. truei* over four times as frequently in stream-adjacent pitfall trap series as in the series located 200 m from the stream. Moreover, *A. truei* captures were similar between stream-adjacent traps and traps at 25 m from the stream but declined sharply from 25 to 75 m and did not differ from 75 to 200 m from the stream. Gomez and Anthony (1996) did not partition post-metamorphic age groups, so how these patterns may differ for adults versus juveniles is unclear. Burkholder and Diller (2007) conducted visual transects (with no estimate of detectability, L. Diller, *pers. comm.*) walking along the stream channel and found that almost all (95%) post-metamorphic *A. truei* captured were within 5 m of the stream. The important perspective here is that assessments of the upslope distribution of adult *A. truei* over long distances (>100 m) from the stream have rarely been attempted.

Adult movement away from streams tends to occur under wet conditions over the broader landscape. The previously noted first observation of post-metamorphic *A. truei* some distance from a stream, which may have involved adults, followed heavy precipitation on the night previous to the survey (Van Winkle 1922). Noble and Putnam (1931) also commented on adults leaving streams during cool wet weather"…several have been captured at such times away from water…" but the importance of the phenomenon was unclear. Metter (1967) also noted that adult *A. truei* leave the vicinity of streams during wet weather. He thought the phenomenon was best illustrated by the population he studied in the Siskiyous of Oregon (his population labelled 10); adults were abundant along the creeks for two nights during a dry period. On the third day, it rained; no adults were found along the creek that night, but two were found on an old road 100 yards from water. Of course, this observation leaves ambiguous whether most

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[181] Gomez and Anthony (1996) used a 200 × 350 m rectangular trap array with the 200-m sides perpendicular and 350-m sides parallel to the stream. All traps were 25 m apart. Traps were opened for 28 days in each of May (cool wet season) and August (hot dry season) in two years (1989 and 1990).

adults moved or not. Bury and Corn (1988a) recognized the importance of wet conditions when they suggested reducing the pitfall trapping interval from 6 months (most of the active season) to no more than 50 days during the fall because trapping efficiency greatly increased during or after precipitation events. However, these suggestions were based on data for mostly juveniles[182] (Bury and Corn 1987). Bury and Corn (1988a) found no relationship between *A. truei* numbers (based on captures in upland pitfall traps) and three moisture classes over 13 old-growth stands ($F_{df(2,10)} = 0.06$, $P = 0.94$).[183] Lack of a relationship may reflect variation in captures across few stands (low power) over two disjunct areas,[184] variation as a function of pitfall trapping,[185] or both. Given that most frogs trapped were juveniles, insight into the movements of adults has remained limited.[186] Because maritime environments are typically more hydric than inland sites, one might expect more overland movements by adults in those environs.

Stream amphibians in the PNW generally have low thermal tolerances (Bury 2008), but specific thermal requirements of adult *A. truei* are not known. Nishikawa and Cannatella (1991) concluded that adult *A. truei* from coastal Oregon maintained at room temperature (20-23°C) seemed stressed based on low feeding rates. Critical thermal maxima ranging from 27.6°C (81.7°F) to 29.6°C (85.3°F) are reported for *A. montanus* adults acclimated to temperatures ranging from 0°C (32°F) to 20°C (68°F; Claussen 1973a), but parallel data for *A. truei* are lacking. Recent data suggest that thermal conditions limiting *A. montanus* larvae may be considerably higher than anticipated (Dunham *et al*. 2007). Adult thermal tolerances cannot be inferred from stream temperature information across the range of *A. truei* because early embryonic stages may be the most limited thermally (see Brown 1975).

Few data exist on age at reproduction for *A. truei*. Burkholder and Diller (2007) estimated that *A. truei* from north coastal California, located toward the southern end of the geographic range, reach sexually maturity at 3 and 4 years for males and females, respectively. This is based on a local one-year larval cycle (Wallace and Diller 1998; see also Bury and Adams 1999), and then 2 and 3 years as a juvenile for males and females, respectively (Burkholder and Diller 2007). Estimates of larval life range up to 4 years toward the northern part of the range (see LARVAL DEVELOPMENT subsection) and juvenile lifespan may also increase, though perhaps not as much as the larval lifespan if data on *A. montanus* provides insight to *A. truei* (Daugherty and Sheldon 1982a). As a consequence, age at maturity would be expected to increase as much as 4 additional years for males (3 additional years of larval life plus one more year as a juvenile) and 5 additional years for females (3 additional years of larval life plus two more years as a juvenile) toward the northern end of *A. truei* range.

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[182] Bury and Corn (1987) used the terminology "young-of-the-year" to refer to recently metamorphosed juveniles.

[183] Bury and Corn (1988a) installed one pitfall array at each site (see footnote 169 and Bury and Corn 1987 for additional details).

[184] Only 13 old-growth stands were used for this analysis, 5 on the H. J. Andrews Experimental Forest (Oregon) and 8 on the Wind River Experimental Forest (Washington).

[185] The distance relationship of pitfall grids to local streams was not described, and orientation of the drift fence arms of the pitfall triads (see footnote 169 and Bury and Corn 1987) depended on openings between trees or large logs on the forest floor.

[186] Though they commented that most trapped frogs were young-of-the-year, Bury and Corn (1987, 1988a) did not present age group-partitioned captures of post-metamorphic animals (i.e., juveniles and adults).

Coastal tailed frogs are thought to emerge at dusk and feed terrestrially at night on small arthropods found along streams and in the damp surrounding forests (Jones *et al.* 2005), but no systematic data exist on the diel pattern of foraging or most details of adult feeding behavior. Fitch (1936) reported a small unidentified brown beetle, a larval geometrid moth, and three small sowbug-like isopods from the stomachs of two adult males taken near the Rogue River (Oregon). Fitch (1936) also noted that the isopods belonged to a species abundant along the creek. Bury (1970) found amphipods the dominant prey, representing 60% of all individuals in the diet of 11 adults from the Trinity region of northern California. A few adult and larval flies (Diptera), stonefly (Plecoptera) nymphs, snails, adult and larval beetles (Coleoptera), adult and larvae caddisflies (Trichoptera), adult moths (Lepidoptera), and millipedes (Diplopoda) were also eaten. Waterstrat and colleagues (2007) found an adult male *A. truei* that had captured an adult male Folding-door Spider, *Antrodiaetus pacificus*, a species often recorded in the PNW riparian forests. Movement away from streams during wet weather previously discussed (e.g., Noble and Putnam 1931, Metter 1967) may be foraging-related. Adult *A. truei* have poorly differentiated tongues, so their approach to prey capture differs from many other frogs in that extension (protraction) of the tongue is much more limited and forward lunging of the body is much more pronounced (Nishikawa and Cannatella 1991, Nishikawa and Roth 1991, Deban and Nishikawa 1992). The speed with which mouth opening, tongue retraction, and mouth closing occur is similar to that of other frogs (Nishikawa and Cannatella 1991), but whether the additional movement needed for forward lunging limits *A. truei* ability to capture selected prey groups is unknown.

Ascaphus montanus: Seasonally, Daugherty and Sheldon (1982a) found *A. montanus* in Montana active (surface visible) from May through September. Based on sampling from July of one year to February of the next in the Wallowa Mountains (Oregon), Bull and Carter (1996a) found *A. montanus* active July through October. However, their sampling likely missed the beginning of the active season because the species was surface active when they began sampling. Nonetheless, Bull and Carter (1996a) found *A. montanus* surface active later into the fall suggesting that the active season in the Wallowas is longer than in central western Montana. However, as Adams and Frissell (2001) noted, Daughtery and Sheldon (1982a) may have also missed part of the active season in their sampling.

Adult *A. montanus* tolerate desiccation poorly. Adults died after losing 28% of their body mass (Claussen 1973a), which is proportionally less mass than all but two of the 30 frog species with which they have been compared (Hillman *et al*. 2000). Intolerance to desiccation is likely an important reason that *A. montanus* is surface active only during periods of time and in habitats that limit water loss. Unlike adult *A. truei*, which have been observed to be diurnal over parts of their geographic range, adult *A. montanus* appear to be exclusively nocturnal (Metter 1964a, 1967; Daugherty and Sheldon 1982a). Metter (1964a) found no adults moving around before dusk unless he disturbed their daytime retreats. At the southernmost location where Metter (1967) studied *A. montanus*, Rocky Bar in Idaho (his population number 17), he found few individuals under the relatively low humidity conditions at dusk. In contrast, he encountered many two hours later, after humidity had increased. Higher daytime air temperatures and lower humidities in *A. montanus* geographic range (in contrast to *A.*

truei geographic range) may help explain this pattern (Metter 1964*a*, Daugherty and Sheldon 1982a). Adult *A. montanus* may typically remain close to the stream for similar reasons including higher humidities and the more hydric nature of the habitat. At his Touchet (Washington) and Palouse (Idaho) study areas, Metter (1964a) found adults up to 12 m (40 ft) from the streams during the few weeks following snowmelt. With onset of summer, no adults were found more than 1 m (~3 ft) from streams. As with *A. truei*, these data need to be viewed cautiously because Metter (1964a) did not clearly define the extent of his search area relative to his study streams. During the day, *A. montanus* adults appear to remain under rocks in the stream, in crevices along stream banks, or in spray-drenched fissures near waterfalls (Metter 1964*a*, 1967; Landreth and Ferguson 1967; Bull and Carter 1996*b*; Daugherty and Sheldon 1982a).

The nocturnal behavior of adult *A. montanus* results in their typically seeking extremely low levels of illumination. In laboratory experiments, when dark-adapted *A. montanus* were given a choice, they almost always sought the dimmest stimulus: between about 1 lux and 10^{-1} lux (Jaeger and Hailman 1973, Hailman and Jaeger 1976). Moreover, typical ambient illumination in *A. montanus* habitat when the species is active, measured near Snowbowl Lodge (Montana), is about 10^{-5} lux (Hailman 1982). This illumination level is 4 or 5 log units below the dimmest stimulus that could be created in laboratory phototactic tests, 1 or 2 log units below what humans perceive as absolutely dark, and comparable to the minimum conditions under which owls can hunt successfully using vision (Hailman 1982).

Movement patterns of adults and the reasons for these movements are the least understood aspects of *A. montanus* life history. Based on the fact that the mainstem between the two smaller creeks at his Touchet study site harbored numerous adults in spring, but few in late summer, Metter (1964a) believed adults moved up the creeks to areas with abundant streambank vegetation increased shade. In an attempt to verify this, Metter (1964a) marked 75 adults, but recovered only two of these animals over a year and a half. Both recaptures were within a few meters of their original points of capture. In a series of displacements experiments with and without the use of visual cues, Landreth and Ferguson (1967) demonstrated that post-metamorphic *A. montanus* orient using rheotactic (streamflow) and celestial cues; though the possibility that other cues were used was not excluded. Both adult and juvenile *A. montanus* were used in these experiments, implying that the orientation mechanism is similar between age groups. In Montana, adults were described as highly sedentary, apparently remaining in a 20-meter stream segment for several years (Daugherty and Sheldon 1982a). Limited movement by *A. montanus* adults led Daugherty (1979) to suggest that recolonization potential is low among their inland-located populations. Daugherty and Sheldon (1982a) also speculated that maintaining small home ranges may help secure food, mates and shelter in an otherwise dry, inhospitable environment. However, Adams and Frissell (2001) suggested that the annual summer sampling that Daugherty and Sheldon conducted may have ended too early to detect a fall migration. Using unidirectional traps associated with a stream weir on Moore Creek (western Montana), Adams and Frissell (2001) captured 32 adult *A. montanus* moving downstream and none moving upstream during September-October 1992. Because they saw no evidence of migration at five other weirs where summer water temperatures remain below 16ºC, they suggested that *A. montanus* may migrate downstream seasonally from upper Moore

Creek to avoid the high temperatures. However, their data are not consistent with migration to avoid peak temperatures and an explanation that addresses avoiding freezing winter temperatures in a relatively low-volume creek may better explain the pattern (see *The Overwintering Season* section).

Few data exist on age at maturity and longevity in *A. montanus*. In northwestern Montana, *A. montanus* may not mature until they are 7 (males) or 8 (females) years old (Daugherty and Sheldon 1982b). Daugherty and Sheldon (1982b) first captured an adult female *A. montanus* in 1973 that they estimated to be a minimum of 10 years old and recaptured her each year through 1977. They speculated that females may live 15 to 20 years and males perhaps less. Sutherland (2000) used these data to estimate average annual adult survivorship at 0.8 because high survivorship is required to achieve longevities of at least 15 years.

Data on diel pattern of foraging or adult feeding behavior are entirely lacking for *A. montanus*. Feeding mechanics of adult *A. montanus* are likely similar to *A. truei* because they also have a rudimentary tongue.

The Overwintering Season

A lack of significant activity is thought to characterize tailed frog overwintering. However, this part of tailed frog life history is the least understood and potentially highly variable. Variability would be expected to reflect differences in temperature and moisture conditions across tailed frog geographic ranges.

Ascaphus truei: Few data exist on *A. truei* overwintering. Coastal *A. truei* adults have been observed to overwinter terrestrially (C. Crisafulli, 2011, *pers. comm.*), but how widespread this pattern may be is unclear. Crisafulli (*pers. comm.*) found several adult-sized *A. truei* beneath the bark debris of a large old-growth Douglas-fir over 50 m from any stream in late fall under freezing conditions after snow had fallen. The occasional finding of adults at concealed terrestrial locations some distance from water in early to late spring may reflect individuals not yet emerged from overwintering (Welsh and Reynolds 1986;[187] M. Hayes, *unpublished data*). Post-metamorphic *A. truei* have been observed during winter stream surveys for Bull Trout (*Salvelinus confluentus*) in the Cascade Mountains of Washington State (K. Aitkin, 2011, *pers. comm.*), but these data have not been analyzed in the context of *A. truei* seasonal life history. Discussing overwintering, Herbert Brown and Lawrence Jones (*pers. comm.* in Bull and Carter 1996b) indicated that *A. truei* adults (and larvae) may burrow into gravel and cobble substrates. Instream overwintering may provide better shelter from extreme winter temperatures, but it may also be risky where high flows mobilize substrates.

Ascaphus montanus: In Butler Creek in Montana, Daugherty and Sheldon (1982a) commented that larvae appear to actively feed throughout the winter. Juveniles inhabit the same streams as adults and can be found in winter under instream rocks. Though snow and low temperatures limit activity, adults were captured swimming in March when the stream was snowbound. In the Wallowa Mountains of northeastern Oregon,

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[187] Welsh and Reynolds (1986) reported an adult (50 mm TL) female found 22 May 1984 15 cm above the ground under the bark of a downed, partly decomposed Tanbark Oak (*Lithocarpus densiflora*) log 40 m from the nearest stream at 1,350 m of elevation in southwestern Oregon.

Bull and Carter (1996b) set up winter study sites on 10 streams.[188] Observation boxes,[189] one each in a pool and a riffle microhabitat in each stream were checked once monthly to characterize flows and search for *A. montanus*. Because the boxes covered such a tiny area of stream, Bull and Carter (1996b) also searched for *A. montanus* in any open water reach within 100 m of the sampling point for 10 minutes per stream.[190] Streams were small and typically covered with 1-2 m of snow, so open water was scarce. As a consequence, only one stream reach was searched in November, two were searched in December and January, and four in February. No *A. montanus* were found in the boxes, but collectively, 21 (9 adults and 12 larvae) were found in the four streams which had open water at some point during the winter. All individuals were found in riffles under rocks <35 cm in diameter and were described as not having burrowed into the stream bed.

Bull and Carter (1996b) suggested that the presence of anchor ice in some streams may preclude their use by *A. montanus* because of the risk of freezing. In the 10 streams they sampled, the water flowed all winter under deep layers of snow, which likely protected the streams from freezing. Dupuis and colleagues (2000) essentially repeated the Bull and Carter (1996b) hypothesis in stating that streams with enough snow cover to prevent them from freezing are key to tailed frog survival in cold climates. Jakober and colleagues (1998) demonstrated that Bull and Cutthroat Trouts made extensive (>1 km [>0.6 mi]) downstream movements with declining temperature in the fall. Once this move had been made, most fish remained stationary until the close of the study in late February, while others made additional downstream movements (1.1–1.7 km [0.7-1.1 mi]) during a low-temperature (≤1°C) interval marked by anchor ice formation. Downstream movements in *A. montanus* during the fall (Adams and Frissell 2001), may represent an avoidance of habitats with a high risk of forming anchor ice. Since the reach in which the movement originated had the highest temperatures, it might also be most vulnerable to the lowest winter temperatures, and thus anchor ice formation.

HABITAT DESCRIPTION AND ASSOCIATIONS

Glenn Sutherland, Linda Dupuis, Tanya Wahbe and Marc Hayes

Suitable habitat is an elusive concept that has been the basis of complex measurement and semantic debate (e.g., Jorgenson 1997, Railsback *et al*. 2003). Ultimately, it means habitat in which a species can persist over a particular time scale, but at least for multiple generations (Huggard 2000). The crux of this concept is understanding the set of conditions that allow persistence given the variability of biotic and abiotic interactions in time and space. A thorough understanding of suitable habitat requires manipulative experimentation at local or regional scales, which for tailed frogs have not been done

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[188] Nine of these streams were known to be occupied based on sampling the previous summer. Surveys were conducted between November 1992 and February 1993 in 7 streams in Union County (Buck, Camp, North Fork of Indian, West Fork of Clark, and East and West Forks of Swamp Creeks), 2 in Baker County (Trout and Big Creeks), and 1 in Umatilla County (Summer Creek).

[189] Observation boxes, made from 1.6-cm thick plywood, were a 60-cm square × 45 cm tall. They had an open bottom, a removable lid, and four 15 cm-long legs made of angle iron that allowed placing the boxes in the stream with the plywood above the water level.

[190] Sampling was conducted by overturning rocks while a dipnet held downstream captured *A. montanus* life stages that were disturbed.

(Kroll *et al*. 2008). Rather, with selected exceptions, what exist are descriptive and retrospective studies that identify habitat variables that may be important to tailed frogs; in some cases, the identified habitat variables may be simply correlated to those of importance. Our approach here is to summarize variables that having been identified by previous studies as being potentially important to tailed frogs, gauge their importance in context of aquatic and terrestrial habitats used by different tailed frog life stages. In this section, we emphasize gaps in and limitations of existing data and where understanding is incomplete, particularly in light of forest management.

Aquatic Habitat

BACKGROUND: Aquatic developmental stages (eggs and larvae) tie both species of tailed frogs to aquatic habitat (see LIFE HISTORY section). Metamorphs, juveniles and adults also appear to be linked to aquatic habitat because they are sensitive to dehydration. We know very little about movement of metamorphs and older frogs in the context of this association. Pitfall traps located at fixed distances from the aquatic habitat seem to imply that animals do not range farther than tens of meters (Gomez and Anthony 1996, Wahbe *et al.* 2004). However, most of these data were not recaptures, so their movement footprint is unknown. Further, where recaptures existed, too few were made to interpret population-level movements and the perpendicular-to-stream orientation of drift fences associated with pitfall trap arrays at or greater than 25 m from the stream could result in an undesirable bias in the direction of recaptures (see Wahbe *et al.* 2004).[191] Few recaptures in this study may suggest that the movement scale of most individuals is substantially greater than the dimension of the drift fence-pitfall arrays (roughly 65 × 100 m; see footnote 170) designed to capture them.[192] Moreover, relatively high vulnerability to desiccation reported for *A. montanus* (Claussen 1973b), which may explain its closer ties to water than *A. truei* (Metter 1967),[193] is confounded with the fact that mesic and riparian habitats are more constrained across *A. montanus* range than across *A. truei* range.

TEMPERATURE: Tailed frogs are generally characterized as requiring streams with cool or cold water temperatures (e.g., Jones *et al.* 2005, Bury 2008), but water temperatures at which various life stages actually become stressed are unknown, and critical thermal limits are available only for a few life stages of each species. Gaige (1920), who worked on *A. truei* over the summer of 1919, likely influenced thinking on its cold water requirements with her statement describing temperatures at an unspecified number of streams in on the Olympic Peninsula (see p. 5 of INTRODUCTION, BACKGROUND AND SYSTEMATICS section), "…these creeks…were…swift, with many falls and miniature

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[191] The drift fence arrays that Wahbe and colleagues (2004) laid out at distances ≥25 m consisted of a 20-m long fence with five 5-m zigzag segments oriented at about 90° angles to each other with one pitfall trap on the inside of each elbow. Three such arrays were set up in a linear series with intervening gaps one 5-m zigzag segment in length between their ends such that the entire series was about 66 m long. One such series was set perpendicular to the stream at each of 25, 50, and 100 m from the stream. As gaps in each series were about one tenth of their length and the width of each array was something less than 5 m, positioning of these arrays alone might increase the probability recapturing individuals moving with versus perpendicular to the stream axis.

[192] This assumes that the drift fence-pitfall approach lacks a general capture bias for these life stages (for example, juvenile and adults have an equal probability of being recaptured or post-metamorphic life stages in general are not trap-shy) and recapture directionality is not biased by drift fence orientation.

[193] Of the 8 populations that Metter (1967) studied, adults were found along the creek after several days of continuous rain in only one, Glacier Park (his population number 11).

rapids, filled with rocks,…and the water was extraordinarily cold, usually under 40°F *(4.4°C)* even on the warmest days (*parenthetical ours*).” Metter (1966) then restated Gaige slightly differently, “Gaige (1920) found *Ascaphus* in streams averaging 4.4°C (40.0°F).” These statements are extraordinary for two reasons: first, Brown (1975) later demonstrated that only 50% of *A. truei* embryos from the mid-elevation North Cascade Mountains of Washington (see p. 48 of LIFE HISTORY section) reared at 5.0°C (41.0°F)[194] survived. He concluded that 5°C (41.0°F) approximates the lower limit of embryonic tolerance. Second, high-resolution (0.5-hr interval) temperature measurements obtained June to September[195] over 4 years (2005-2008) in 13 *A. truei*-occupied non-fish-bearing streams from the same area in which Gaige (1920) did her work reveal water temperatures from 5.8°C (42.4°F) to 16.3°C (61.3°F) and a range among individual streams that exceeds 8°C (14.4°F; M. Hayes, *unpublished data*). Metter (1966) also noted that others had collected *Ascaphus* in streams ranging from 5°C (41.0°F) to 15°C (59.0°F).[196] He added that Noble and Putnam (1931) could not find the species in streams above 16°C (60.8°F), though their actual statement was, “Above timber line streams containing *Ascaphus* may reach a maximum temperature of 16°C…”, a temperature they recorded on 27 August. These data are consistent with Brown’s (1975) demonstration, also based on mid-elevation North Cascade Mountains animals, that *A. truei* embryos die if exposed to water temperatures of 19°C (66.2°F) or higher, and his estimate that the critical maximum temperature for embryos was about 18.5°C (65.3°F). The statement that led to emphasizing water temperature as critical for Coastal Tailed Frogs was that of Brown (1975), who stated that the range of temperatures that their embryos tolerate (specified as 5°C [41.0°F] to 18.5°C [65.3°F]) had both the narrowest range and lowest maximum of any North American frog. Further, data on embryonic limits collected since that time for numerous other frogs around the world would support that statement, extending it to all frogs globally for which limiting temperature data are available. Investigators since Metter (1966) and Brown (1975) have documented temperatures for *A. truei*-occupied streams in summer, the interval when embryos would be anticipated, to

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[194] Five degrees Centigrade (41.0°F) was the lowest temperature at which Brown (1975) reared *A. truei* eggs. He reared eggs at constant temperatures ranging from 5°C (41.0°F) to 21°C (69.8°F).

[195] This interval encompasses both *A. truei* oviposition and embryonic development (see LIFE HISTORY section), which is the period of time with the warmest stream temperatures annually.

[196] This statement of Metter (1966) could represent a combination of both species since it was made many years before the two species were recognized, but data on water temperature collected prior to Metter (1966) applied almost exclusively to *A. truei*. The only published temperature data provided for an *A. montanus*-occupied stream between when Gaige (1920) recorded her observations and Metter (1966) wrote his paper were those of Corbit (1960), who obtained a temperature of 9°C (48.2°F) at 11:30 hr in the headwaters of Trail Creek (Valley County, Idaho) and 11°C (51.8°F) at 12:30 hr 6.4 km (4 mi) downstream. A few investigators provided temperature data on *A. truei*-occupied streams over this same period. On 3 September 1931, Svihla and Svihla (1933) recorded an *A. truei*-occupied tributary of the Snoqualmie River roughly 16 km (10 mi) east of North Bend, Washington to be 10°C (50.0°F) at 13:00 hr. The most substantive data were those of Ricker and Logier (1935), who reported 10-12°C (50.0-53.6°F) minima and 11-14ºC (51.8-57.2°F) maxima based on daily measurements taken over the interval 5 June-12 September 1934 from Smith Creek, an *A. truei*-occupied stream near Cultus Lake, British Columbia. We do not doubt that “numerous” investigators collected *Ascaphus* in streams ranging from 5°C (41.0°F) to 15°C (59.0°F) over this period (Metter 1966), but only those noted above reported water temperatures. The rest either provided only a qualitative assessment of the thermal condition of the stream, i.e., cool or cold (for what is now *A. truei*: Myers 1931, 1943; none for what is now *A. montanus*) or did not comment on its thermal condition at all (for what is now *A. montanus*: Rodgers and Jellison 1942; Slipp and Carl 1943; Manville 1957; Grant 1961; for what is now *A. truei*: Slater 1931; Linsdale 1933; Fitch 1936; Slipp and Carl 1943; Carl 1949, 1955; Carl and Cowan 1945). Brattstrom (1963) erroneously attributed to Noble and Putnam (1931) the statement that, "Water temperatures above 14°C (57.2°F) are apparently beyond the tolerance of these [tailed] frogs."

fall within the 5°C (41.0°F) to 18.5°C (65.3°F) range that Brown (1975) proposed as the thermal limits for embryos.[197] Embryonic thermal limits for *A. montanus* are unknown, but may differ from those of *A. truei* based on the probable differences in the thermal requirements of larvae of the two species (addressed in the next paragraph).

Water temperature data for larval tailed frogs indicate that differences likely exist in the temperature requirements of the two species. In thermal selection experiments conducted in the laboratory, de Vlaming and Bury (1970) showed that larval *A. truei* selected temperatures between 0°C (32.0°F) and 22°C (71.6°F), avoiding temperatures >22°C (>71.6°F).[198] These data generally agree with the finding of Hawkins and colleagues (1988) that differences in larval *A. truei* densities in their study basins,[199] which had maximum temperatures around 20.0°C (68.0°F),[200] did not suggest adverse effects in streams in which the higher temperatures were recorded. However, de Vlaming and Bury (1970) found that regardless of acclimation temperature,[201] modal temperatures selected by 1st-year larvae (3-8°C [37.4-46.4°F]) were always lower than those selected by 2nd-year larvae (12-16°C [53.6-60.8°F]), which may indicate that elevated temperatures are stressful for 1st-year larvae.[202] Hawkins and colleagues (1988) speculated that the relatively high larval densities in the warmer lower reaches[203] of their headwater-forested streams was due to dispersal from upstream sites into downstream reaches with abundant food. At northern latitudes, rain-fed streams appear to support greater larval *A. truei* production than colder snowmelt- or glacier-fed streams (L. Dupuis, *unpublished data*), likely because their warmer water temperatures enhance larval growth through greater instream production. This finding has also been proposed to explain why *A. truei* larvae were most common in streams among harvested stands in west-central Oregon where unharvested forest remains upstream (Bury and Corn 1988*b*; Corn and Bury 1989). If correct, this would suggest that larvae benefit from increased within-stream production mediated at least in part by increased temperature resulting from local clearcut harvest.

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[197] Welsh (1990) recorded *A. truei* in 28 of 39 streams in coastal northwestern California and southwestern Oregon, in which the highest spot water temperature of occupied streams recorded was 14.3°C (57.7°F). Adams (1993) recorded summertime (July-August) spot water temperatures of 13.0-14.5°C (55.4-58.1°F) at *A. truei* oviposition sites in southwestern Oregon.

[198] Larval *A. truei* were obtained from French Hill Creek, Del Norte County, California.

[199] Hawkins and colleagues (1988) sampled 13 headwater basins over the years 1985 to 1987. Basins were similar in size (5-10 km^2) and average slope (15-20%), but differed in extent of disturbance caused by the 1980 eruption. In 6 basins, the forest was blown down and all vegetation killed. In 3 basins, forests in the lower basins were destroyed, but trees in the upper basins (30-50% of total basin) were not killed. Vegetation and streams in 4 remaining basins received heavy ash fall, but vegetation was not destroyed. Eight to 13 of the basins sampled each year because of time constraints and access to sites.

[200] Temperature data were based on reading and resetting maximum-minimum thermometers weekly that were placed in each stream over the interval mid-July-early September 1986. Maximum temperatures Hawkins and colleagues (1988) reported were based on means of this weekly point data collected over this interval. Mean maximum water temperatures were not reported for individual streams, but for groups of streams in the non-forested, headwater-forested, and forested basin categories described in footnote 144. For these basin categories, mean maximum water temperatures were 19.5°C (67.1°F), 17.2°C (63.0°F), and 13.5°C (56.3°F) respectively. They also assumed that the differences observed among sites in temperatures in 1986 reflected relative differences among sites in general (i.e., over the three years sampled).

[201] Acclimation temperatures were 5ºC (41.0°F), 10ºC (50.0°F), and 16ºC (60.8°F) for experimental runs for each of first- and second-year larvae. Acclimation at 12ºC (53.6°F) and 21ºC (69.8°F) was also done prior to runs for first-year larvae.

[202] Both 1st- and 2nd- year larvae represented older larvae, that is, with fully developed mouthparts and typical darker coloration; 1st-year larvae do not correspond to the younger larvae described in the LIFE HISTORY section.

[203] Just how Hawkins and colleagues (1988) made this assessment is unclear since they stated that, "We measured water temperatures only in the lower reaches of each watershed."

However, in southwestern British Columbia, Wahbe and Bunnell (2003) found larval density and biomass highest in headwater streams where, among other variables, temperature was lowest; latitude cannot explain this. Further, on the Olympic Peninsula, Adams and Bury (2002) found that *A. truei* density increased as temperature decreased. Larval abundance also appeared low in streams with the highest temperatures (>14.3ºC) in northwestern California (Welsh 1990). In this case, the greater risk of streams attaining stressful temperatures in this southern landscape makes sense, but selected patterns linked to temperature appear to be modulated by unrecognized or unmeasured variables and/or the absolute temperature range in various stream reaches may be important in explaining differences. That *A. montanus* larvae might tolerate higher temperatures than *A. truei* was first suggested from the observations of Adams and Frissell (2001), who found larvae numerous in water 19.5-20.0ºC (67.1-68.0ºF) but also present in water 21.0ºC (69.8ºF) in Moore Creek, Montana. Still, they viewed these observations conservatively, speculating that *A. montanus* larvae may use the cooler microhabitats in local seeps to avoid the generally warmer stream water. Dunham and colleagues (2007) provided more support for the idea that larval *A. montanus* tolerate higher temperatures than larval *A. truei*. Based on work in Idaho,[204] *A. montanus* was widespread (in 94% of streams) regardless of water temperatures, which ranged up to 26.6ºC (79.9ºF). Further, their plot of larval *A. montanus* captures as a function of maximum water temperatures suggested that they were common[205] across the observed temperature range (11.9-26.6ºC [53.4-79.9ºF). Also, Dunham and colleagues (2007) found little evidence of cold-water refugia at their 100-m sampling scale, but they granted undetected refugia might exist at smaller scales.

Few data exist on the temperature requirements of adult tailed frogs. Nishikawa and Cannatella (1991) found that adults appeared stressed and fed poorly when maintained at room temperature (20-23ºC [68.0-73.4ºF]). Metter (1966) conducted temperature trials[206] on adults that may have been *A. montanus* based on where he completed his work (Metter 1964a), but uncertainty exists because Metter did not specify the origin of the animals used in those trials. In his fluctuating temperature trials (see footnote 206), no animals died when 25ºC (77.0ºF) was the maximum temperature, whereas one male and one female died when 28ºC (82.4ºF) was the maximum temperature, and all 12 adults used in the trial died when 31ºC (87.8ºF) was the maximum temperature. By comparison, all the adults died between 18 and 30 hours in the steady temperature trial where the temperature was maintained at 22ºC (71.6ºF) for 48 hours. These data indicate that temperatures of at least 22ºC (71.6ºF) are stressful and potentially lethal with sufficiently long exposure, but adults may survive temperatures of 25-28ºC (77.0-82.4ºF) where exposure is probably something less than nine hours. The approach in the fluctuating temperature trail was to increase the temperature over the first nine hours, but Metter (1966) did not specify the

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[204] Ninety streams were sampled; 60 were located in landscapes that had been burned. Half the streams in burned landscapes (n = 30) were selected because they had sustained significant channel re-organization.

[205] Common was regarded as >10 individuals per site, where a site was a 100-m sampling reach that was four-pass-removal electroshocked.

[206] Before testing, animals were acclimated at 10°C (50°C) for 3 days. Six females and 6 males were used in each trial. Two types of trials were run: a fluctuating temperature trial and a steady temperature trial. The fluctuating trial involved reaching a target temperature over 9 hours then cooling to 10°C (50.0°F); the steady trial involved slowly raising the temperature to 22ºC (71.6°F), maintaining it for 48 hours, then cooling it to 10°C (50.0°F). In the fluctuating trial, the temperature target was 25°C (77.0°F) on the first trial, 28°C (82.4°F) on the second and 31°C (87.8°F) on the third. Observations were made hourly and animals were held for several days to identify potential delayed mortality.

pattern of increase, so the actual interval over which 25-28ºC (77.0-82.4ºF) temperatures are tolerated could be substantially shorter than nine hours. Given the questions about the potential dissimilarity between *A. truei* and *A. montanus* as the result of the work of Adams and Frissell (2001) and Dunham and colleagues (2007), the species attribution of Metter's 1966 work should be regarded cautiously.

Additional systematic temperature data for adult *A. montanus* were provided by Claussen (1973a), who reported mean critical thermal maxima (CTM) for *A. montanus* that ranged from 27.6°C (81.7ºF) to 29.6°C (85.3ºF). Most variation that Claussen observed appeared attributable to the acclimation temperature that was used.[207] Within extreme limits, higher acclimation temperatures resulted in higher critical thermal maxima. Claussen also found that the incipient lethal water temperature[208] for adult *A. montanus* ranged from 23.4ºC (74.1ºF) to 24.1°C (75.4ºF). When provided with a 4.0ºC to 27.0°C (39.2ºF to 80.6°F) temperature gradient from which to choose, Claussen (1973a) discovered that the mean temperature selected by *A. montanus* when they were individually tested was 17.1ºC ± 2.6°C (62.8ºF ± 4.7°F). Interestingly, temperatures selected were significantly lower (14.2ºC ± 2.7°C [57.6ºF ± 4.9°F]; $P < 0.05$), when *A. montanus* were tested in groups of five to 10.[209] Notwithstanding the lack of comparability of temperature tolerance data, available information implies that both the CTM for adult *A. montanus* and temperatures

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[207] Claussen (1973a) collected adult *A. montanus* from a tributary of Butler Creek near the Missoula Snow Bowl (ca. 1,524 m [5,000 ft] elevation), Missoula County, Montana. This stream had temperatures that ranged from 0ºC (32.0ºF) to 9.5ºC (49.1ºF) annually. Frogs were acclimated for 3-5 days to 0ºC (32.0ºF) or 10ºC (50.0ºF) prior to separate trials, and 7-9 days at 20ºC (68.0ºF) before a third trial. Claussen used 8 adults in each of the 0ºC (32.0ºF) and 10ºC (50.0ºF) trials, and 6 adults in the 20ºC (68.0ºF) trial. Methods for determining CTMs were similar to those of Brattstrom (1968). After a 1-hr at a moderate temperature to avoid thermal shock, frogs were placed in an insulated test chamber containing 4 cm of water and heated with an overhead heat lamp attached to a rheostat, at a rate of 1°C(1.8°F)/min until the CTM was reached. Loss of righting response without subsequent recovery when the frog was placed in cool water was used as the end point criterion.

[208] Claussen (1973a) acclimated adult *A. montanus* used in the incipient lethal water temperature trials for 1 week at 10ºC (50.0ºF). To avoid thermal shock, animals were placed at room temperature for 30-min prior to each trial, and then moved to 4000-ml glass test chambers. For each trial, 6 *A. montanus* were placed in each chamber, which contained a 200-ml water dish embedded in wet sand. A Pasteur pipette and a thermistor were introduced into each chamber through holes in a removable plastic lid. Air, pre-heated to chamber temperature, was introduced through the pipette and slowly bubbled through the water in the dish. The thermistor monitored chamber temperature. Each chamber was immersed in a circulating water-bath maintained at the desired temperature. Chamber temperature remained within 0.l°C in all cases. Frogs were checked periodically and those that failed to respond to prodding with a metal probe were recorded as "dead". Each "dead" frog was removed and placed in cool water to assess possible recovery. Each trial was terminated when 5 out of 6 *A. montanus* were recorded as "dead". Claussen ran 4 trials, with temperatures respectively maintained at 24.1ºC (75.4ºF), 24.4ºC (75.9ºF), 25.6ºC (78.1ºF) and 25.8ºC (78.4ºF), Except for one female (the second *A. montanus* to "die" at 25.6°C [78.1ºF]), no frog recovered when placed in cool water. Hence, the end point criterion was essentially equivalent to physiological death.

[209] Claussen (1973a) used a styrofoam-lined wooden frame (326 cm × 28 cm basal inside dimensions). A flat double coil of aluminum tubing across the long axis of the styrofoam so was embedded flush with its surface. The tubing, connected one end of each of these two coils to a water pump in a constant temperature bath, was insulated with foam rubber. Cold fluid, 8:1 water to anti-freeze, was pumped through this coil at a rate of 55-60 ml/min. At the opposite end of the gradient chamber, the fluid was heated by passing it through an aluminum coil immersed in a second constant temperature bath. The emerging hot fluid was then returned to the cold water-bath via the second flat coil. The resulting counter-current heat exchange facilitated maintaining the thermal gradient. Adjusting the water-bath temperatures and rate of fluid flow established the desired gradient. The base and embedded coils were covered with a thin layer of wet sand (about 20% water by weight) to provide a uniform substrate, to facilitate heat dispersal and to avoid dehydrating tested frogs. Frogs were tested either individually or in groups of 5 or 10. Frogs were tested both with no gradient (control), and in two somewhat different thermal gradients (see Claussen 1973a for details). Substrate temperature was constant to within 1°C (1.8°F) and air temperature to within 2°C (3.6°F) at any gradient position during each experiment. Fine-gauged thermocouples were used to measure the temperature of the gradient at a particular point and the resulting body temperature of a frog at that point.

that *A. montanus* adults select voluntarily exceed those for *A. truei*. In a reach-scale analysis of variation in *A. montanus* larval density, heat load index (see Beers et al. 1966) appeared in the best model for analyses on both Youngs and Mica Creeks (Jones 2008), though it had the greatest effect as a predictor variable only on Youngs Creek. As heat load index increase with a SW flowing aspect, A. montanus larval density decreased significantly when the closer Youngs Creek flowed toward a southwest direction.

INORGANIC SUBSTRATE: Numerous investigators have characterized instream tailed frog habitat as possessing an unconsolidated or unattached inorganic substrate fraction that is coarse-grained. Coarse inorganic substrates provide a larger and perhaps more stable matrix of instream spaces than their finer-grained counterparts (Dupuis *et al.* 2000) or most organic substrate alternatives. Based on tailed frog life history (see LIFE HISTORY section), such a matrix has at least three functions:[210] 1) oviposition and rearing habitat for eggs and embryos; 2) foraging habitat for larval stages; and 3) refuge habitat for all mobile life stages (meaning all life stage except eggs and embryos).

For *A. truei*, the clast size distribution of coarse inorganic substrates most frequently utilized ranges from large gravels to small boulders (these represent descriptive labels based on the Udden-Wentworth scale[211]). Experimental work has revealed that *A. truei* larvae from coastal western Oregon selected substrates in the range of 55 mm to 125 mm (large gravels to small cobbles; Altig and Brodie 1972). Additionally, the field data of Hawkins and colleagues (1988) from the South Cascade Mountains of Washington revealed that disproportionately greater numbers of *A. truei* larvae were recorded where clast sizes were 11-30 cm (large cobbles to small boulders). Utilization of larger-grained substrates than Hawkins and colleagues (1988) found in the field may reflect Altig and Brodie’s excluding large-cobble-to-boulder-sized clasts from their selection matrix, even though certain other factors, such as the size of larvae examined, could have contributed. Based on her examination of 10 streams in British Columbia, the percentage of instream cobble (65-256 mm) was the only inorganic substrate factor that Wahbe (1996) found positively correlated with the biomass and density of *A. truei* larvae.[212] Moreover, based on 54 streams in northwestern British Columbia, Dupuis and Steventon (1999) reported that the densities of larval *A. truei* were positively correlated with rubble ($r = 0.69$).[213] In

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[210] Among tailed frogs breeding and oviposition activities are temporally separated, so a coarse inorganic interstitial matrix may also provide breeding habitat, a condition that seems to be supported by a very limited number of observations of breeding animals in the field.

[211] We provide descriptive labels for clast size information based on the Udden (1914)-Wentworth (1922) scale because descriptive labels provided in the various studies are frequently not comparable. All clast size information is provided as maximum diameters.

[212] The Pearson product-moment correlation coefficient (r) for the relationship between cobbles and both biomass and density of *A. truei* larvae was >0.63. Coefficients for the relationship between biomass or density and all other clast sizes was less than the absolute value of 0.54; all of were non-significant.

[213] Rubble was defined as angular material in a categorization set separate from particle sizes, but the intent was to have rubble include all inorganic angular particles of the size of gravel or larger. For this study, Dupuis and Steventon (1999) selected three permanent road-accessible creeks in each of three treatments (old-growth [unharvested], clear-cut harvested with no buffers, and clear-cut harvest with 5-60 m forested buffers) within six drainages (experimental blocks) for a total of 54 creeks. Drainages included Carpenter, Kleanza, Shannon, and Trapline Creeks; and the Clore and Copper Rivers, all located in the Hazelton Mountains. Three 5-m reaches were searched on each stream, with the first randomly placed, the next two 50 m apart. Searches included an initial scan for surface-active animals, followed by an in-depth search of all creek substrates: hand-raking sand and gravel, upturning cobbles and small boulders, sweeping large boulder surfaces by hand, and scanning the moist banks. Searches began at the downstream end of the reach, and proceeded upstream in 1-m increments. Dip nets were placed immediately downstream of surveyors to capture dislodged animals.

a microhabitat survey which examined 17 streams, Diller and Wallace (1999) found the percentage of small cobble (65-128 mm) to be the second most explanatory among four variables in a stepwise logistic regression model designed to explain the presence of *A. truei*.[214] Adams and Bury (2002) also found a strong positive association between *A. truei* density and a cobble substrate in Olympic National Park. This analysis differed from previous ones in that while larvae were the dominant life stage sampled, post-metamorphic frogs were included in the analysis. In an analysis encompassing a British Columbia-wide dataset,[215] Sutherland and Bunnell (2001) identified the clast size distribution of the stream substrate as the most important predictor of *A. truei* density (37.0% of the original deviance); the second most important predictor, lithology, explained only 22.0% of the original deviance (see LITHOLOGY section).

By contrast, fewer analyses of clast size distribution exist for *A. montanus*. Observations made in the Flathead River drainage in Montana led Franz and Lee (1970) to make the qualitative observation that streams with large slab-like flat-bottomed rocks support more *A. montanus* larvae than those with smaller irregular or smooth-edged round rocks. Working in the Blue-Wallowa Mountain complex of eastern Oregon and Washington, Bull and Carter (1996*a*) found that a two-variable stepwise regression model using amount of instream clasts 5-30 cm (large gravels to small boulders) and ≤0.3 cm (small gravels or smaller)[216] best predicted larval abundance. However, their rather modest adjusted co-efficient of determination (r^2_{adj} = 0.36) indicates that most variation explaining larval abundance was unidentified. Moreover, the basis for small clast sizes appearing as a positive predictor of *A. montanus* abundance in their model is unclear; small clast sizes appear negatively related to *A. truei* abundance based on several analyses (next paragraph). If real, that relationship may represent another way in which *A. montanus* differs from *A. truei*. Bull and Carter (1996*a*) also developed a regression model to predict adult *A. montanus* abundance in which two coarse clast variables (amount of cobbles and amount of boulders) in a four-variable model were positive predictors of abundance (stream buffer presence and slope were the other two). Again, a modest co-efficient of determination (r^2_{adj} = 0.36) indicates that most variation in abundance was not identified. Using a mixed model approach with larval density as the response variable, Jones (2008) found cobbles as the most important predictor variables in each of the Youngs and Mica Creek systems.

For *A. truei*, instream habitat with distributions of clast sizes generally both smaller and larger than the large-gravel/small-boulder range are avoided or less frequently used. Altig

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[214] Diller and Wallace (1999) surveyed 349 1.5-m belts for this effort. The original basis for developing the model was drawn from a 15-variable set. High gradient riffle (one of several habitat types scored) was the variable with the greatest explanatory power (positive association with *A. truei* presence), the remaining two variables with some explanatory power were low gradient riffle (positive association), and percent fines (negative association). Since the percent correct classification in the 4-variable model (81%) was only 4% greater than the percent correct classification in the model with only high gradient riffle (77%), Diller and Wallace (1999) ran a second model omitting habitat type as an independent variable. This model also found small cobble (positive association) as the second most explanatory of 4 variables. The most explanatory variable in this case was percent fines (negative association) and the remaining two variables with some explanatory power were water depth (negative association) and large boulders (positive association).

[215] Sutherland and Bunnell (2001) georeferenced 864 records of tailed frog occurrence, abundance, and habitat from 3 sources: an extensive survey across the range of tailed frog habitat in British Columbia collected by Linda Dupuis, and two intensive studies of habitat associations in replicated forest management treatments (Wahbe 1996).

[216] Bull and Carter (1996a) termed the sizes of clasts 5-30 cm and ≤0.3 cm in diameter, respectively, cobble and fines. However, 5-30 cm on the Udden-Wentworth scale spans the range between large gravels and small boulders, whereas ≤0.3 cm encompasses the lower end of gravels downwards.

and Brodie (1972) experimentally determined that *A. truei* larvae avoided substrates ≤36 mm (small gravels or finer). Hawkins and colleagues (1988) found disproportionately fewer *A. truei* larvae where clast sizes were relatively small (≤10 cm; small cobbles or finer) or very large (>30 cm; coarser than the lower end of boulder range). Dupuis and Steventon (1999) found a relatively strong negative relationship between the percentage of fine sediments and densities of larval *A. truei* (r = -0.80). In particular, they recorded larval *A. truei* densities in streams with ≥40% fine sediments to be less than one fourth of that in streams with <40% fine sediments.[217] In a reach-scale assessment based on a stepwise regression,[218] Diller and Wallace (1999) found a negative association between percent fines (which they defined as the substrate fraction finer than sand) and *A. truei* presence as one of three variables to enter the model (the other two were stream gradient [positive association] and water temperature [negative association]). Yet, based on strict interpretation of the rejection criterion they chose ($\alpha = 0.05$), none of these variables were significant.[219] However, in separate microhabitat-scale analysis also using stepwise regression (see footnote 214), Diller and Wallace (1999) found a negative association with fines to be the least important of four significant variables predicting *A. truei* presence. Wilkins and Peterson (2000) found that the streams in which *A. truei* larvae were detected had less sand (≤2 mm) than streams where they were not detected. Wahbe and Bunnell (2003; see also Wahbe 1996) reported that density and biomass of larval *A. truei* were highest in streams lacking silt and the percentage of sand was lowest. In particular, they reported biomass and densities of *A. truei* larvae over three- and four-fold greater, respectively, at sites without versus with silt; and over two- and three-fold greater, respectively, at sites with low (≤10%) versus high (>10%) levels of sand.[220] As noted in the previous paragraph, the only study addressing the relationship of fine substrates to *A. montanus* is that of Bull and Carter (1996*a*), which, unexpectedly, revealed a positive relationship to larval abundance - a finding that begs for clarification.

Embeddedness, which describes the degree to which coarse substrates are embedded in fine ones (see footnote 146), has been linked to the negative relationship between *A. truei* occurrence or abundance and fine substrates. Near Mt. St. Helens, Hawkins and colleagues (1988) believed that patterns of embeddedness (and forest loss) best explained the variation in densities of *A. truei* larvae. Notably, they found disproportionately more larvae where embeddedness was ≤80%, and speculated that few refuges (little interstitial

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[217] Precisely what Dupuis and Steventon considered fine sediments is slightly confusing since the finest substrate category they recorded was sand, which they defined as including all inorganic substrates with particle diameters <2 mm. Moreover, they stated that, "Tadpole densities were more than four times higher in creeks with <40% fine sediment than in creeks with large amounts of sand and pebbles [= gravel as treated in this review]." Nonetheless, Dupuis and Steventon intended that fine sediments refer to particle sizes smaller than the range of sand based on the Udden-Wentworth Scale, that is ≤0.0625 mm dia (L. Dupuis, personal observation).

[218] Diller and Wallace (1999) used a stratified random selection approach to select up to four sections per township, ensuring that at least one section per 1/4 township (9 sections) was selected. Each section chosen was at least one half of the target ownership (Green Diamond) and had road access. Within the chosen section, the first 1st- or 2nd-order stream encountered along the major road through the section that had at least 1000 m of channel with flowing water was sampled. Fifty-four sample streams were selected in this manner. Fixed stream reaches were located 10 m above the roadway or culvert. Cross-stream transects, based on (Platts *et al.* 1983) were placed at 5-m intervals starting 2.5 m above the lower end of the reach and 10 transects were established in each sample stream unless physical features (waterfalls, log jams, subsurface stream) prevented it. In one stream, only 25 m (five transects) were sampled, but in all other streams at least 30 m (six transects) were sampled.

[219] Fines (P = 0.051), gradient (P = 0.051), and water temperature (P = 0.084).

[220] Wahbe and Bunnell (2003) scored silt as present versus absent whereas sand was scored as a percentage of the standard Udden-Wentworth scale similar to all larger instream substrate categories.

space) exist in streams where embeddedness was high. Welsh and Ollivier (1998) evaluated sedimentation effects (Croke and Hairsine 2006 for a review)[221] on *A. truei* larvae in 10 streams after a major storm in the Coast Redwood ecosystem of northwestern California. Highway bypass construction had impacted five streams; remaining unimpacted streams served as references. Both sediment depth and embeddedness was greater in impacted versus unimpacted streams. In unimpacted streams, tailed frog larvae were more abundant in riffles and step runs compared to other habitats, whereas in impacted streams, larvae were more abundant in pools and glides. Welsh and Ollivier (1998) interpreted this difference to mean that larvae had reduced access to the interstitial matrix because sediment fills those spaces. However, larvae were more abundant in pools and glides, which seems counterintuitive since sediment tends to accumulate to a greater degree in those habitats. They also noted that larvae were impacted even in habitats that were less sedimentation prone, a result suggesting that something besides the loss of interstitial spaces affected tailed frog abundances in impacted streams. They speculated that sedimentation might limit larval food resources.

Coarse inorganic substrate matrices represent a basic aspect of habitat structure for both species of tailed frog, though more work is clearly needed to better understand the importance of this structure to *A. montanus*. The abundance of fine sediments and embeddedness are likely positively correlated and measuring elements along the same niche axis. However, what remains unclear is whether some threshold of embeddedness or some proportion of fine substrate exists below which aquatic habitat is still suitable. This understanding could also clarify the basis of the positive relationship that Bull and Carter (1996a) recorded between larval *A. montanus* abundance and fines. Lastly, though cobble-sized material has been frequently linked to suitable habitat for *A. truei*, perhaps because of the relationship to oviposition habitat (Karraker *et al.* 2006), correlations between substrate clast sizes and the sizes of different tailed frog life stages imply greater complexity in refuge requirements. Understanding life-stage specific requirements for interstitial refugia may elucidate how different inorganic clast size combinations influence habitat suitability. In Jones' (2008) reach-scale analysis of *A. montanus* larvae abundance in Youngs and Mica Creeks, embeddedness appeared as a variable in the best fit model for both creek systems. However, the embeddedness variable for the best fit model for Mica Creek, which was described as moderately loose embeddedness, had a significant positive effect on larval density. This result seems unexpected, and may indicate that the positive relationship between larval *A. montanus* abundance and fines that Bull and Carter (1996a) may not be extraordinary, but an understanding of its basis needs to be explored.

ORGANIC SUBSTRATES:[222] Several researchers have investigated the relationship between tailed frogs and organic instream substrates, but the results are difficult to interpret. Some analyses have incorporated non-wood organic substrates. In northwestern British Columbia, Dupuis and Steventon (1999) found that the densities of larval *A. truei* were inversely correlated with increasing levels of detritus (r = -0.72), which they defined as

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[221] To evaluate sedimentation in each stream, Welsh and Ollivier (1998) sampled pools. Sediment depth was measured at three points in each pool (upstream end, middle, and downstream end) and averaged. Welsh and Ollivier (1998) also visually estimated the percentage of embedded coarse substrate at the tail of each pool.

[222] Includes all categories of organic material originating from vegetation, ranging from large wood to branches and twigs to litter.

fine organic debris.[223] In contrast, in north coastal California, Diller and Wallace (1999) found that small organic debris[224] had too little explanatory power to enter any of the models they developed to explain *A. truei* presence or abundance at either reach or microhabitat scales. Similarly, a landscape "microscale" analysis[225] using classification and regression tree (CART) analysis revealed that fine organic debris was not included in models for either *A. truei* occurrence or abundance (Sutherland *et al.* 2000). In a more formalized CART analysis, Sutherland and Bunnell (2001) found that fine organic debris explained only two percent of the original deviance in an *A. truei* occurrence model, and lacked explanatory power to enter models involving *A. truei* measures of abundance. As the Sutherland and Bunnell (2001) analysis represented a quasi-meta-analysis, it remains unclear how differences in data collection methods among the three studies may influence the ability to identify the importance of fine organic debris to *A. truei* occurrence and abundance patterns. Furthermore, organic debris[226] was removed from Adams and Bury (2002) stream-associated amphibian habitat analysis for Olympic National Park because it was correlated with variables with greater explanatory power and that seemed better connected to *A. truei* life history.

Analyses of wood are also inconsistent. Dupuis and Steventon (1999) found densities of larval *A. truei* inversely correlated with levels of wood (r = -0.80).[227] They also found wood strongly positively correlated (r = 0.93) with organic detritus (previous paragraph). Similar to their perspective on small organic debris (previous paragraph), Diller and Wallace (1999) found wood[228] an unimportant variable in models explaining *A. truei* presence or abundance at either reach or microhabitat scales. In an analysis that combined life stages, Adams and Bury (2002) described a significant relationship between coarse woody debris (CWD) and *A. truei* density where the latter peaked at 10% CWD cover. Whether these different *A. truei* relationships to wood are rooted in geographic patterns, detectability issues, or other factors is unclear.

Clear patterns between organic debris and frog abundance across the range of tailed frogs are currently not evident. The lack of patterns may arise from study constraints, as some addressed solely unmanaged landscapes (e.g., Adams and Bury 2002), others addressed exclusively timber-managed landscapes (e.g., Diller and Wallace 1999), and some addressed both (e.g., Sutherland and Bunnell 2001). In managed landscapes, slash and woody debris have been regularly reported to almost completely obscure small streams (Dupuis and Steventon 1999, Jackson *et al.* 2007), whereas in unmanaged landscapes, the percentages of woody debris cover in the stream rarely exceeds 25% (Adams and Bury

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[223] Dupuis and Steventon (1999) recorded detritus as low (0-2 mm deep, in <10% of the reach substrate), medium (0-2 mm deep, in 10-50% of the reach substrate), high (on >50% of the substrate, water column stained), or extreme (opaque water column).

[224] Diller and Wallace (1980) defined small organic debris as total linear length of leaves, twigs, and sticks <10.2 cm in diameter on the substrate.

[225] The analyses of Sutherland and colleagues (2000) were landscape-scale, the subscales of which were defined by the range of detectable spatial autocorrelation in the original variables (macro = 80–120 km; meso = 25–60 km; micro < 25 km). Sutherland and colleagues (2000) did not incorporate wood into their analysis; data on wood were only available for a portion of their composite dataset.

[226] Adams and Bury (2002) defined organic debris as organic debris other than coarse wood. Their coarse wood was the large wood debris (>5 cm dia) of their earlier analyses (Bury and Adams 2000).

[227] Dupuis and Steventon (1999) estimated the percentage of wood debris (>1 cm in diameter) within a reach and categorized it as little (<10%), low (10-30%), medium (31-50%), high (51-80%) and extreme (>80%).

[228] Diller and Wallace (1980) defined wood (or large organic debris) as total linear length of dead woody material >10.2 cm in diameter occurring over or in the stream, but not on the streambed.

2002). Equally important, detectabilities, unmeasured in these studies (Kroll *et al*. 2008), might be expected to decrease as levels of organic debris increase. For example, whether *A. truei* densities actually decrease as CWD levels increase above 10% (Adams and Bury 2002) is unclear if individual detectabilities also decline as levels of CWD increase.

CHANNEL GEOMORPHOLOGY: Generalizing across populations of both species of tailed frogs, Dupuis (1999) suggested that the step-pools morphology in headwaters provided the most suitable *Ascaphus* breeding habitat. However, Karraker and colleagues (2006) recorded more oviposition sites for both *A. montanus* and *A. truei* in riffles than in pools (see LIFE HISTORY SECTION for details), though how the step-pools of Dupuis fit into this classification is unclear. If tailed frog oviposition sites are accessed (i.e., detected) more easily in riffles than steps-pools, an unexamined consideration, the data of Karraker and colleagues (2006) may not conflict with Dupuis' suggestion. Understanding the true relationship between channel geomorphology and tailed frog habitat will require better understanding of the relative use of different in-channel habitats of the more cryptic tailed frog life stages. Clearly, both tailed frog species also occupy pool-riffle habitats characteristic of lower gradient (often fish-bearing) streams or cascade-pool habitats where permanent boulder/log accumulations occur at points of constriction within a channel (see Grant *et al*. 1990 for details). Step-pool habitats typically arise where bed materials (including logs) are large relative to the size of the channel, providing local stability and serving to dissipate stream energy and regulate channel hydraulics (Chin 1989; Grant *et al*. 1990). Stability of the step-pool morphology at small temporal and spatial scales is the basis of Dupuis' (1999) suggestion regarding their habitat suitability in headwater streams. In larger streams, step-pools morphology changes in response to discharge and sediment load associated with debris flows and floods occurring on the order of 5-to-100-year intervals (Chin 1989; also see Lamberti *et al.* 1991). Given that *Ascaphus* are known to be able to recolonize streams within two to three years following channel disturbances at some sites (see Richardson and Neill 1995; Dupuis and Friele 1996), step-pool habitats may be suitable for *Ascaphus* larvae regardless of stream size. Evaluating the life-stage specific response of tailed frogs to channel disturbance type and frequency will be needed to fully evaluate the relative importance of channel morphology to tailed frog habitat.

BIOTIC INTERACTIONS: Biotic interactions are among more poorly known aspects of tailed frog life history. In the context of aquatic habitat, the biotic interaction that has garnered the greatest attention is the trophic relationship between primary production, tailed frog larvae and other instream grazers. To date, available data have addressed exclusively *A. truei*. Using in-stream manipulations and experimental channels near Mount St. Helens, Lamberti and colleagues (1992) evaluated the grazing impact of two large benthic herbivores, larvae of *A. truei* and *Dicosmoecus gilvipes* (a caddisfly),[229] and assessed whether grazing intensity reflected disturbance history. In an initial experiment, *A. truei* larvae were stocked in nine experimental channels[230] at densities ranging from 0 to 96/m²

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[229] Species selection was based on their abundance/dominance in the local stream herbivore guild.

[230] Each channel was 1.80 m long × 0.28 m wide × 0.13 m deep, fed by gravity through PVC pipes with water from the adjacent stream, filtered through an inclined, self-cleaning 250-µm-mesh screen into a header box before delivery to the channel. The screen removed macroinvertebrates and large particulates and, but allowed passage of algae and small invertebrates. Flow was maintained at 16 L/min (4.2 gal/min) and a water depth of 5 cm (2 in) using a standpipe and a current velocity of 2 cm/sec (0.8 in/sec).

(0 to 8.9/ft^2).[231] Gross primary production and grazing impacts in these channels were assessed using unglazed tiles.[232] Algal biomass, chlorophyll a, and the density of benthic invertebrates declined significantly with increasing larval *A. truei* density.[233] In a second experiment, in-stream platforms[234] were used to reduce grazing by larval *A. truei* on tile substrates in 11 small, high-gradient streams differential affected by the 1980 volcanic eruption.[235] Single platforms erected in each tributary showed only minor grazing effects relative to grazed controls, and no significant differences were found among streams varying in their disturbance intensity (and hence tadpole density). However, Lamberti and colleagues (1992) believed that variability among streams in factors other than the abundance of *A. truei* larvae probably confounded this experiment. In a third experiment using five platforms/stream, Lamberti and colleagues (1992) examined two unshaded streams, one with relatively high *A. truei* larvae densities (5 larvae/m^2 [0.5 larvae/ft^2]) versus one lacking larvae. In the larvae-occupied stream, grazing reduced the biomass of periphyton and chlorophyll *a*, respectively, by 98% and 82%. In the stream lacking larvae, no significant grazing effects were evident. The low algal abundance on treatment and control platforms, and high invertebrate density (ca. 30,000/m^2) in the stream lacking *A. truei* larvae suggests that grazing by small vagile invertebrates was about equivalent to that of *A. truei* larvae. The value of the Lamberti and colleagues' (1992) study was that it indicated that the influence of grazing by *A. truei* larvae on primary production and invertebrate grazers appeared density-dependent.

Based on data using 12 experimental channels in southwest British Columbia,[236] Kiffney and Richardson (2001) showed that grazers (*A. truei* larvae and invertebrates) and periphyton were resource-limited. Resource limitation was shown by manipulating the presence of *A. truei* larvae and nutrients. Periphyton (based on ash-free dry mass) was significantly higher in nutrient-supplemented channels. *Ascaphus truei* larvae in nutrient-

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[231] This experiment was conducted in the unshaded floodplain of one of the basins forested only in its headwaters (see footnote 144 and Hawkins and colleagues [1988]). One year *A. truei* tadpoles were stocked at densities 0, 4, 8, 16, 24, 32, 48, and 96 m^2 (0, 0.4, 0.7, 1.5, 2.2, 3.0, 4.5 and 8.9 ft^2).

[232] Eighteen square 55 cm^2 (8.5 in^2) unglazed tiles were place in each channel on 3 cm (1.2 in) of clean gravel about 3 cm (1.2 in) apart. The experiment lasted 26 days and all sampling occurred at the end of the experiment. For benthic algae analysis, six randomly chosen tiles were removed from each channel, three of which were analyzed separately for each of algal biomass and chlorophyll *a* abundance. Another three tiles randomly selected from each channel were used to analyze benthic invertebrates.

[233] For algal biomass, $r^2 = 0.56$, $P < 0.001$; for chlorophyll a, $r^2 = 0.59$, $P < 0.001$; and for benthic invertebrates, $r^2 = 0.50$, $P < 0.05$.

[234] Platforms consisted of 625-cm^2 (97-in^2) metal plates raised 10 cm (4 in) above the streambed but still submerged and supporting nine 55-cm^2 (8.5-in^2) clay tiles, a method that Lamberti and Resh (1983) described. This design reduced grazing by less mobile benthic invertebrates, but drifting and swimming herbivores were less affected. Control platforms were identical but placed directly on the substrate to allow access to all herbivores.

[235] Five streams were in totally deforested subbasins, three streams were within entirely intact forest, and three streams had intact forest only in their headwaters (upper 20-40% of the subbasin). Larval *A. truei* densities also varied with forest condition, unforested basins had low densities ($\bar{x} = 0.6$ larvae/m^2 [0.1 larvae/ft^2]), forested streams had moderate densities ($\bar{x} = 2.7$ larvae/m^2 [0.3 larvae/ft^2]), and headwater forested streams had high densities ($\bar{x} = 4.4$ larvae/m^2 [0.4 larvae/ft^2]). However, streams were similar in average gradient (15-20 percent), drainage area (5-10 km^2 [1.9-3.9 mi^2]), channel substrate composition (cobble dominated), and discharge (summer baseflow, 0.1 m^{3}s^{-1} [3.5 ft^{3}s^{-1}]).

[236] Kiffney and Richardson (2001) used channels 15 m long × 0.20 m wide located on a floodplain next to 3rd-order perennial stream (Mayfly Creek). Channels were mostly unshaded to minimize the likelihood of light limitation. Water came from 100 m upstream and passed through two settling boxes and a final headbox to stabilize flows. Channels, which averaged 3% in slope, were lined with plastic and natural substrata (sand, gravel, and cobble) arranged in an alternating sequence of slow-velocity riffles and runs. Flow, roughly 0.5 L/sec during the 38-day study, did not differ among channels.

supplemented channels had growth rates about four times higher than larvae in non-supplemented channels.[237] Furthermore, evidence of competition among grazers was reflected by insect grazer abundance being lower when *A. truei* larvae were present regardless of nutrient supplementation. However, in the latter cases, the reduction in insect grazer abundance was greater in nutrient-supplemented channels. Mallory and Richardson (2005) experimentally altered light, nutrient levels, larval *A. truei* density and enclosure size to examine their effects on periphyton standing crop in two headwater streams in southwestern British Columbia. They concluded that periphyton was light-limited in both streams, but overall, levels of periphyton were greater in Dipper Creek than in Klondike Creek.[238] The basis of this difference was unclear, but either higher ambient nutrients in Dipper Creek or somewhat higher water temperatures (potentially inhibiting periphyton growth, resulting in higher *A. truei* grazing rates, promoting faster turnover of algal biomass or some combination thereof) in Klondike Creek might be responsible. However, nutrient supplementation had but minor effects despite the low ambient levels of phosphorus and nitrogen. This response appeared puzzling given that Kiffney and Richardson (2001) observed the aforementioned fourfold increase in larval growth rates with nutrient supplementation in streams that had lower ambient nutrient levels than these study streams. Mallory and Richardson (2005) emphasized that these contrasting results point to environmental context being pivotal to understanding complex outcomes. Further, they demonstrated that grazing by larval *A. truei* significantly reduced periphyton standing crop in both streams. Larval densities in their study streams were at the low end of the manipulated density gradient, which agrees with the idea that larvae growth is density-dependent. Regulation of periphyton production also differed between streams. In particular, grazing by larval *A. truei* was a more important control of periphyton standing crop than light level at Klondike Creek, but the magnitude of these effects was reversed at Dipper Creek. Larval growth was faster at Klondike than at Dipper Creek despite lower levels of periphyton in the former. Mallory and Richardson (2005) attributed this difference to the fact that warmer temperatures in Klondike Creek

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[237] Kiffney and Richardson (2001) collected 60 *A, truei* larvae from Mayfly Creek and added 10 to each of six channels (three of which had received nutrients) for a density of 3.3 m^2, within the range found in natural streams per Hawkins and colleagues (1988; 0.58–4.4 m^2). Larvae were weighed and measured at the beginning and end of the study. No initial differences existed in larval size among channels ($P = 0.1$). Experiment day 0 was the day larvae were added to channels. Nutrients were added using slow-release fertilizing pellets to increase phosphorus, which Kiffney and Richardson (2001) hypothesized limited periphyton biomass because channels were in near full sunlight. In these pellets, phosphorus was in the form of phosphate; nitrogen was ammonia nitrogen. To attain 5 μg/L dissolved phosphate based on flow rates, Kiffney and Richardson added 88.5 mg of pellets to six channels, three of which received larvae, beginning one week prior to the addition of larvae.

[238] Mallory and Richardson (2005) provided two levels of light (shaded, unshaded), two levels of nutrients (ambient, elevated), three levels of enclosure size (small, medium, large), and six levels of larval *A. truei* density. They built enclosures from PVC pipes halved lengthwise with their ends and top covered with 1-mm mesh to retain larvae and allow water exchange and light influx. Three enclosure sizes allowed a broader range of larval densities. Small enclosures (0.035 m^2 in area), a design modified from Lamberti & Feminella (1996), were randomly assigned no, one, two or three larvae resulting in densities of 0, 29, 57 or 86 larvae/m^2. Medium (0.070 m^2) and large (0.105 m^2) enclosures were two and three times larger, respectively, than small ones. Medium and large enclosures provided one larva each enabled densities of 14 or 10 larvae/m^2, respectively. A set of medium enclosures each provided with 2 larvae and large enclosures each provided 3 larvae enabled a density directly comparable to that in small enclosures with one larva. Four replicates of small enclosures and two replicates each of the medium and large enclosures existed for each treatment combination in each stream. Light was manipulated using industrial shade cloth, which reduced levels 85-90%, similar to mature or second-growth forest. Nutrients were manipulated using slow-release pellets placed 10 m upstream of half of the enclosures (midpoint of study reach) as nutrients could not be applied randomly to enclosures.

facilitated depression of algal production by *A. truei* larvae, inducing higher algal turnover rates.

Overall, studies addressing primary production emphasize context-dependent outcomes. To date, all manipulative studies addressing primary production that may influence *A. truei* larvae have been conducted at relatively high latitudes in the northern half of *A. truei* geographic range. These studies have demonstrated that periphyton may be resource limited, via light or nutrients. These results may not apply at lower latitudes, where light may be less limiting, and higher biodiversity may provide greater nutrient loading. Additionally, high latitude streams in British Columbia may be predator depauperate (e.g., generally no giant salamanders), and as Mallory and Richardson (2005) point out, the density-dependent limitation of *A. truei* growth rates they observed may only occur when predators are rare and thus do not strongly affect *A. truei* foraging rates. At lower latitudes, *A. truei* may be less limited by low temperatures or not at all and more elevated water temperature may somehow become limiting. How this different set of limitations may interact with available light, nutrients and a different predator set is unknown.

The remainder of what is known about biotic interactions relates to predators. Direct observations of predation are largely anecdotal and extraordinarily rare (Cope's Giant Salamander and American Dipper on larval *A. truei*: Nussbaum *et al.* 1983, Morrissey and Olenick 2004; Idaho Giant Salamander and Wandering Garter Snake on larval *A. montanus*; Metter 1963, 1964a; see LARVAL DEVELOPMENT subsection under LIFE HISTORY section for details). The relative importance of such predators can be implied only from their apparent abundances in PNW headwater streams (e.g., Adams and Bury 2002 for Cope's Giant Salamander), though in some cases, large seasonal fluxes in their abundances may occur (e.g., Morrissey *et al.* 2004 for American Dipper). Behavioral experiments reveal species-specific responses to potential predators (Feminella and Hawkins 1994), which makes understanding population-level responses to predation difficult without understanding of local predator sets and the relative importance of the individual predators that comprise them. For example, Adams and Bury (2002) reasonably postulated that predation by Cope's Giant Salamander could negatively affect other instream amphibians on the Olympic Peninsula, but found no relationship between the density of *A. truei* and that of Cope's Giant Salamanders.[239] However, the density of *A. truei* larvae in the five major drainages without Cope's Giant Salamanders was greater than in eight of the nine drainages in which they were present (Adams and Bury 2002),[240] which suggests that Cope's Giant Salamander may in fact be limiting. At least some of the responses of *A. truei* larvae to presence of predators in an experimental context (Feminella and Hawkins 1994) are confounded with behavioral responses to physical factors (light, temperature). Further, measures of injury no doubt reflect predator pressure (Blair and Wassersug 2004), but address only those individuals that evaded predation. These studies show that both the correct context and scale of predation is critical to interpreting its impacts.

Recently, Kroll and colleagues (2008) found that *A. truei* occupancy was negatively correlated with crayfish presence (specifically Signal Crayfish, *Pacifastacus leniusculus*) over a broad study area across western Oregon and Washington. Because Signal Crayfish

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[239] Adams and Bury (2002) reported a probability value of 0.361 for this relationship.

[240] Adams and Bury (2002) did not record Cope's Giant Salamanders in the Dosewallips, Elwha, Gray Wolf, Morse, and Lyre drainages of the northeast Olympic Peninsula.

are widespread in the PNW (Bondar *et al.* 2005) and non-native crayfish prey on stillwater amphibians (Gamradt and Kats 2002, Cruz *et al.* 2006), this amphibian-native crayfish relationship in lotic aquatic habitats deserves attention.

Data addressing interactions with potential predators for *A. montanus* are sparse. Based on Idaho Giant Salamander diet (see LIFE HISTORY section for details), Metter (1963) provided a few data. His data suggest that larval *A. montanus* are important in the diet of large individuals, but whether either the availability of *A. montanus* larvae affects Idaho Giant Salamander survival or reproduction or whether the salamander somehow limits *A. montanus* abundance or distribution is unknown. More recently, Jones (2008) found fish presence significant positively associated with larval *A. montanus* density in Mica Creek in Idaho. However, Jones (2008) also found fish presence negatively associated with the density of *A. montanus* larvae in Youngs Creek, Montana, but the latter relationship was not significant. Jones (2008) concluded that the positive association between fish and larval *A. montanus* density reflected the local abundance of the benthic-dwelling mottled sculpin (*Cottus beldingi*), which is known to associate with substrates similar to those *A. montanus* larvae use (Swanson *et al.* 1998). Brook trout (*Salvelinus fontinalis*) were present in both systems, but appeared more limited in Mica Creek, leading Jones (2008) to conclude that the positive association between fish and *A. montanus* larvae probably reflected the relationship with the sculpin rather than for the non-native trout species, which is known to negatively affect amphibians elsewhere (Vredenburg 2004).

STREAM SIZE: Tailed frogs have been reported across a relatively broad range of stream sizes, but relationships to stream sizes are difficult to interpret because studies have consistently limited the range of potential stream sizes considered. In British Columbia, *A. truei* has been surveyed in streams ranging from 0.5 to 15 m in wetted width (Dupuis and Friele 1996, Wahbe 1996, Dupuis and Bunnell 1997). In a study focused on the Hazelton Mountains, Dupuis and Steventon (1999) found that densities of *A. truei* larvae were positively correlated with bank width ($r^2 = 0.48$) for streams up to 6 m in bank width, but this relationship disappeared when overall coastal British Columbia was examined (Sutherland 2000). Sampling across Olympic National Park in streams ranging from 0.6 to 5.3 m in width, Adams and Bury (2002) found that *A. truei* densities had a quadratic relationship with width such that densities peaked at stream widths just below 3 m. In a study that selected lower-order streams (3rd-order and lower) in which bankfull width did not exceed 6 m, Kroll and colleagues (2008) also found that *A. truei* density had a quadratic relationship to stream width with peak densities at widths between 4 and 5 m. The effect of stream size on *A. truei* is likely indirect but it is unclear what factors drive observed relationships. Whether the density peak is related exclusively to a physical relationship (e.g., substrate clast size; see Brummer and Montgomery 2003), a limiting biotic relationship (either more predators or greater predator diversity downstream; Reeves *et al.* 1998), or some combination of these is unknown. The precise limiting conditions may also vary geographically.

Ascaphus montanus have been reported to inhabit smaller streams, up to 4 m in wetted width (Franz and Lee 1970; Dupuis and Wilson 1999). Though stream size has not been studied in the same way as for *A. truei*, Dupuis and Friele (2006) provided evidence for *A. montanus* densities peaking at a relatively small basin sizes. Analyses of Jones (2008) in Idaho and Montana reinforce this pattern, indicating that though *A. montanus* larvae have been recorded in streams of fairly large size, larval densities peak where streams sizes are relatively small. Because basin size is strongly correlated with stream size, the quadratic pattern suggested for *A. truei* may also apply here.

STREAM GRADIENT: *Ascaphus truei* occurs in streams across a wide range of gradients, and identifying a relationship to stream gradients has been elusive. In British Columbia, Dupuis and Steventon (1999) found no relationship between larval *A. truei* density and gradient.[241] In a reach-scale analysis in northwestern California, Diller and Wallace (1999) found gradient to be one of only three of an original 21 variables included in a logistic regression model predicting *A. truei* presence (the other variables were percent fines and water temperature), although some question existed as to the statistical significance of the variable.[242] Still, Diller and Wallace (1999) noted that gradient was the only reach-scale variable that differed significantly between reaches where larval *A. truei* were found versus not detected (gradients were higher in the former). Using British Columbia data at a micro-landscape scale (see footnote 215), Sutherland and Bunnell (2001) found gradient (expressed as reach slope) had too little explanatory power to appear in CART models addressing *A. truei* occurrence, relative abundance or density. Gradient as expressed by stream slope was not in Welsh and Lind's (2002) regression models addressing larval and adult abundance of *A. truei*. Gradient seems to have little ability to explain *A. truei* abundance in a simple way; and an ability to explain *A. truei* presence, as the Diller and Wallace (1999) analysis seems to point, may be the result of a sampling artefact.

Where broader sampling across the landscape has been attempted, a complex relationship between *A. truei* and gradient emerges. Using data from across Olympic National Park, Adams and Bury (2002) modeled a 3rd-order relationship to gradient in which *A. truei* density peaks just below 25% and rises again above 60%. However, this curve has only one point with a gradient above 60%. More recently, sampling across western Oregon and Washington, Kroll and colleagues (2008) found a quadratic relationship between *A. truei* occupancy and gradient, with the likelihood of occupancy highest at intermediate gradients. These patterns generally indicate that *A. truei* is less frequent and less abundant in streams with the lowest (<5%) and highest (>50%) gradients.[243] Low-gradient streams generally have less stream power and may less effectively flush fine sediments that accumulate in interstitial spaces (Murphy and Hall 1981), which in turn may limit the number of refuges for *A. truei*. This phenomenon is more common in low gradient streams that support more predators than high gradient streams (Reeves *et al.* 1998). In contrast, high-gradient streams (typically low-order headwater streams) are conducive to frequent bedload movement events (Dietrich and Dunne 1978, Benda 1990, Lancaster *et al*. 2001), which may render them relatively inhospitable to tailed-frogs compared to streams having intermediate gradients (see HABITAT STABILITY subsection under the LOCAL AND REGIONAL LANDSCAPE FEATURES section).

Few stream gradient data exist for *A. montanus. Ascaphus montanus* populations in British Columbia occur in relatively lower gradient streams, averaging 4% (Dupuis and

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[241] Dupuis and Steventon (1999) correlated larval density (as the natural logarithm of larval density plus 1) against gradient (% slope). The co-efficient of determination was extremely low ($r^2 = 0.004$).

[242] Diller and Wallace (1999) reported a $P = 0.051$.

[243] Unfortunately, comparison between the peak in the relationship between *A. truei* and gradient between Adams and Bury (2002) and Kroll and colleagues (2008) cannot be made because of the tabular details addressing gradient in the latter report were unavailable.

Wilson 1999). Dupuis and Wilson (1999) suggested that the steeper headwaters in this region tend to be ephemeral and/or subject to high bedload transport that may restrict *A. montanus* to streams with lower gradients. In the Blue Mountains of northeastern Oregon, Bull and Carter (1996*a*) found gradient to be one of four variables in a stepwise regression model predicting the abundance of post-metamorphic *A. montanus* (buffer presence and amount of instream boulders and cobbles were the other three variables). Abundance had an inverse relationship to gradient but sites were limited to gradients between 5% and 20%. The similarity between the Bull and Carter (1996a) and Dupuis and Wilson (1999) data, obtained at opposite ends of *A. montanus* geographic range, may indicate that more frequent occurrence or greater abundance at lower gradients is a general pattern for this species in contrast to *A. truei*. We remain cautious in this interpretation because if ephemeral hydrology limited the use of higher gradients in the Bull and Carter (1996a) study as it may have done in that of Dupuis and Wilson (1999), then the low gradient pattern would break down where *A. montanus* was not hydrologically limited.

Terrestrial Habitat

BACKGROUND: Semi-aquatic or terrestrial life stages (metamorphs, juveniles and adults) utilize stream-adjacent terrestrial habitat and make moves of varying length across that habitat under conditions that remain poorly understood (see LIFE HISTORY section).

RIPARIAN ZONES: Little work has been done on terrestrial habitat associations of the post-metamorphic life stages of tailed frogs. Aubry (1997) captured post-metamorphic *A. truei* in pitfall traps in all sampled age classes of PNW managed forests, but recorded them most frequently in stands 10-20 years old.[244] This finding may reflect greater instream primary production associated with more open canopies of younger forests, but this interpretation could be confounded by juveniles and adults using different-aged forests. Post-metamorphic *A. truei* were excluded from the final analyses of this work (Aubry *et al.* 2004), presumably because of too few captures (see Aubry 1997). Based on a regression analysis, Bosakowski (1999) found post-metamorphic *A. truei* significantly associated with mature and pole conifer stand types,[245] but low capture rates limits confidence of this conclusion.

Bull and Carter (1996*a*) found that presence of a stream buffer was one of four variables that best predicted adult *A. montanus*[246] abundance (the other three were slope [gradient] and each of the amount of instream boulders and cobbles). The importance of a stream buffer relative to the other three variables cannot be evaluated because their regression co-efficients were unavailable for comparison.

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[244] Aubry (1997) did not partition post-metamorphic age classes for this analysis.

[245] Bosakowski (1999) developed multiple regression models for 11 species, including *A. truei*, which addressed eight habitat associations: mature conifer, pole conifer, sapling conifer, recent clear-cuts, alder-hardwoods, brush, rock, and open wetland. This work, conducted on the 21,600 ha Murray Pacific Corporation Mineral Tree Farm in Lewis County (Washington), involved examination of 50 streams, 29 wetlands, and 8 talus slopes over the years 1994 to 1996. This analysis was based on 43 post-metamorphic *A. truei*, all of which were found in some of the 50 streams. As with the Aubry (1997) study, post-metamorphic age groups (juveniles versus adults) were not partitioned. During stream surveys, surveyors worked upstream searching shallow water, splash and flood zones, and adjacent stream banks up to 30 m from the stream. Surveyors, equipped with potato rakes, overturned large (>10 cm) rocks, logs, and bark piles in a survey approach that was a modification of Corn and Bury (1990).

[246] The adult category of Bull and Carter (1996a) included post-metamorphic juveniles.

VEGETATION ASSOCIATIONS: Other than the fact that tailed frogs occur exclusively in forested landscapes, neither species appears linked to specific vegetation associations *per se*. Metter (1964a) commented that differences in vegetation between his Palouse and Touchet study sites[247] indicate that the range of *A. montanus* is not correlated with any specific plants. Dupuis and Wilson (1999) commented that *A. montanus* was restricted to spruce-fir forests, but that comment addressed Canadian populations exclusively, which encompass only the relatively small northern portion of its geographic range.

In California, Bury (1968) repeated Metter's view for *A. truei*, which he recorded in four vegetation associations.[248] Similarly, Diller and Wallace (1998) recorded *A. truei* from two vegetation associations in northwestern California, Coast Redwood and Douglas-fir, but found no significant difference in *A. truei* occupancy between associations ($P = 0.682$). Other statements made about vegetation associations have been general and reflective largely of geographic or physiographic regions. Though Bury and colleagues (1991*a*) found no significant relationship between forest stand moisture level and *A. truei* abundance (see also Aubry and Hall 1991), the species was recorded most often in stands categorized as either wet or having intermediate levels of moisture.[249] In the Oregon Coast Ranges, *A. truei* was not detected in stands categorized as dry (Corn and Bury 1991).[250] Sampling three areas across the north-to-south latitudinal moisture gradient on the west slope of the Oregon Cascade Mountains, Gilbert and Allwine (1991) found *A. truei* most often (40 percent of all captures) at the most moist (northernmost) sites and least often at the driest (southernmost) sites.[251] Descriptions of stands across this gradient exist, but presence of specific plants in those stands has not been associated with *A. truei* presence or abundance.

In British Columbia, Dupuis and colleagues (2000) found the distribution of *A. truei* to be largely congruent with that of the Coastal Western Hemlock Zone. However, they also indicated *A. truei* range extended into the wetter portions of the Interior Douglas-fir Zone, was found at scattered sites in the Mountain Hemlock and Engelmann Spruce-Subalpine Fir Zones, and had been reported from one location in the Alpine Tundra Zone.

A relationship between non-canopy vegetation and *A. truei* abundance has occasionally been noted. Corn and Bury (1991) obtained a significant positive relationship between the percent cover of forbs and *A. truei* abundance ($P < 0.01$) in the Oregon Coast Range, but the significance of that finding was not discussed. Similarly, Welsh and Lind (2002; see also Welsh 1993) found a positive relationship between herb cover and adult *A. truei* abundance ($P = 0.006$) in northwestern California, which they viewed as related to moist conditions, particularly those associated with late-seral forest (next paragraph). However,

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[247] Western Red Cedar (*Thuja plicata*)-Western Hemlock forest dominated his Palouse study site, whereas a mixed Grand fir (*Abies grandis*), Douglas-fir, and Western Larch (*Larix occidentalis*) forest dominated his Touchet study site (Metter 1964a).

[248] In California, Bury (1968) found *A. truei* in Sitka Spruce (*Picea sitchensis*), Coast Redwood, Douglas-fir, and Ponderosa Pine (*Pinus ponderosa*) forests.

[249] Bury and colleagues (1991a) used the categorization that Spies and Franklin (1991) developed to place old-growth stands into moisture classes. Spies and Franklin (1991) used ordination analyses of the species composition of stands to reevaluate their relative moisture condition.

[250] Corn and Bury (1991) did not record *A. truei* in dry stands, even dry stands in old growth, and found them more abundant in stands categorized as wet than in stands with intermediate levels of moisture ($F_{2,24} = 10.5$, $P = 0.001$).

[251] Gilbert and Allwine (1991) sampled clusters of sites on each of the Mt. Hood National Forest (northernmost geographic location), H.J. Andrews Experimental Forest on the Willamette National Forest (intermediate geographic location), and Rogue and Umpqua National Forests (southernmost geographic location).

their low co-efficient of determination (r^2 = 0.171) reveals that this relationship explains only a small proportion of the variation they observed in abundance. Whether the forb or herb understory is directly linked to *A. truei* life history or is correlated to other variables influencing *A. truei* abundance remains unclear.

Arguably one of the most discussed associations among tailed frogs is the relationship between *A. truei* and late-seral forests that Welsh (1990) first proposed. Discussing both *A. truei* and the Southern Torrent Salamander (*Rhyacotriton variegatus*), Welsh (1990) stated, "The long-term, close association and exact distributional correspondence with these ancient forest types imply that *these amphibians have coevolved with habitats existing only within these forests*" (italics ours). Late-seral forests unquestionably provide habitat suitable for *A. truei* in portions of their geographic range, but arguing that such habitats exist exclusively within such forests contradicts available data. In the Cascade Mountains of southwestern Washington, Aubry and Hall (1991) found *A. truei* adults significantly more abundant in mature forest stands than in either older or younger stands.[252] Further, on the west slope of the Cascade Mountains in Oregon, Gilbert and Allwine (1991) found post-metamorphic *A. truei* exclusively in old-growth stands at their southernmost (lowest latitude) sites (see footnote 251), whereas they were most frequent in mature stands at the intermediate geographic location, and most frequent in young stands at the northernmost site.[253] Even over *A. truei* range in California, where climatic conditions are anticipated to result in a closer association between *A. truei* and late-seral forest, the relationship is not absolute because the maritime climate of coastal locations can attenuate drier conditions associated with young forest stands (Diller and Wallace 1999). Available data indicate that, all else being equal, suitability of terrestrial habitat for *A. truei* tend to become more closely tied to late-seral forest at low latitudes and interior locations, where climatic conditions presumably promote this association. That is, late seral forests provide better microclimate (i.e., more mesic conditions). As one moves toward wetter climes in the PNW, that is, generally toward coastal locations or to higher latitudes, suitable terrestrial habitat conditions for *A. truei* become available over a broader range of forest conditions. In fact, the data that Aubry and Hall (1991) and Gilbert and Allwine (1991) provided suggest that at higher latitudes, late-seral conditions are less often used because they are more likely to be limiting light to streams needed to support primary production. These data appear consistent with studies demonstrating that primary production is light and/or nutrient limited in streams at higher latitudes (see BIOTIC INTERACTIONS SUBSECTION, p. 84) as well as studies revealing that forestry practices effects on *A. truei* are not the same across the species' geographic range (see SECTION on POTENTIAL EFFECTS OF FORESTRY PRACTICES, p. 96).

Lack of broad forest type associations does not exclude the possibility that tailed frog ranges may be associated with non-canopy plants, an idea unexamined rangewide for either species. In south-coastal British Columbia, Matsuda (2001) reported that the numbers of adult *A. truei* trapped were negatively correlated to the percent cover of species characteristic of clear-cuts (Red Elderberry [*Sambucus racemosa*, $r = -0.28$],

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[252] Aubry and Hall (1991) used three categories of forest stands (age range in years in parentheses): young (55-75), mature (80-190), and old (210-730). The average age of each stand was determined by growth ring counts from increment coring or examination of cut stumps in nearby stands (Spies *et al.* 1988).

[253] Gilbert and Allwine (1991) used three stand age categories (age range in years in parentheses): young (30-80), mature (80-200), and old-growth (>200).

Salmonberry [*Rubus spectabilis, r* = -0.26], Thimbleberry [*Rubus parviflora, r* = -0.28], and thistles [*Cirsium* sp., *r* = -0.34]), whereas numbers of recent post-metamorphs (= the immatures of Matsuda [2001]) trapped were positively correlated with Foamflower (*Tiarella trifoliata, r* = 0.48) and Fireweed (*Epilobium angustifolium, r* = 0.31). Given these associations were based on small sample sizes (Matsuda 2001) and the highest coefficient of determination (r^2) in the lot is 0.23, these patterns may simply reflect life-stage specific responses to the physical habitat with which these plants are associated.

WOODY DEBRIS: Few studies have exampled the relationship between wood and tailed frogs in a terrestrial context. In Washington, Aubry and Hall (1991) found no relationship between wood and post-metamorphic *A. truei* in unmanaged forests. Also in Washington, Aubry (2000) found no evidence that variation in amphibian abundance was strongly influenced by the amount of coarse woody debris on the forest floor of second-growth managed stands, although sample size for post-metamorphic *A. truei* (n = 15) were low. Data are lacking in California, where one might expect wood to potentially take on greater importance to *A. truei* as refuge in a terrestrial environment that appears frequently less suitable. Welsh and Lind (2002) measured several aspects of forest stands in context of post-metamorphic *A. truei,* but woody debris was not measured.

Other Features

BACKGROUND: "Other Features" address factors that either fit poorly into either aquatic or terrestrial habitat categories or apply to both.

CLIMATE: Selected aspects of climate may seem like obvious features that might limit the distribution of tailed frogs, but few studies have evaluated the relationship of climate to tailed frog distribution. Bury (1968), the first to evaluate how climate might limit *A. truei* distribution, showed that its distribution in California was restricted to areas with over 100 cm (40 in) of precipitation annually. The amount and seasonal distribution of rainfall also appears to be linked to the dispersion and size of *A. truei* populations in British Columbia, though the causal basis of this relationship is unclear. In a regional analysis, Sutherland (2000) demonstrated that *Ascaphus* populations in British Columbia are found in areas of moderate annual precipitation (>120 cm [47 in]) with relatively high summer precipitation levels (30-80 cm [12-31 in]), though these relationships were difficult to separate from the effects of other correlated variables. Along a longitudinal transect across the British Columbia coast, a pattern seems to exist in the dispersion of populations. The windward side of the Coast Ranges has small and scattered populations, whereas on the leeward side, populations are large and widespread (Dupuis *et al*. 2000). This shift in densities coincides with a marked shift in levels of annual precipitation, which are about twice as high on the windward side of the Coast Mountains (279 cm [110 in] versus 145 cm [57 in]; Meidinger and Pojar 1991, Dupuis *et al*. 2000).

In contrast, Adams and Bury (2000) found *A. truei* tadpole abundance in the Olympics was positively associated with greater local heating (degree days) and lower precipitation. They believed that these relationships reflect factors governing broad distribution patterns and may have less to do with these variables considered in isolation. Since absolute precipitation levels over areas of the Olympic Peninsula sampled by Adams and Bury (2000) range from over 508 cm (200 in) to as little as 76 cm (30 in), *A. truei* on the Olympic Peninsula may be responding to the inhibitory effects of high precipitation (as well as the correspondingly cooler temperatures) that Dupuis and colleagues (2000) reported for northwestern British Columbia, a region where the absolute precipitation range is relatively high.

In companion studies addressing the degree of genetic exchange among regional populations of each of *A. truei* and *A. montanus*, Spear and Storfer (2008, 2010) found the counterintuitive result that genetic differentiation was less in the relatively more xeric habitat of *A. montanus* than the more mesic habitat of *A. truei*. Moreover, precipitation never appeared as an explanatory variable among their best models for *A. truei* but was prominent as an explanatory variable among the best models for *A. montanus*. Their interpretation that precipitation levels are more likely to be limiting for *A. montanus* makes sense, but the counterintuitive genetic differentiation patterns imply non-parallel responses to climatic variation between the two species.

HABITAT STABILITY: Recolonization of a stream following channel disturbance can occur within two to three years (Dupuis and Friele 1996), presumably by adults that could avoid the disturbance through escape into adjacent terrestrial habitat. Following the 1980 eruption of Mount St. Helens, key components of both plant and animal communities recovered to pre-disturbance levels within three to five years (Hawkins *et al.* 1997; Crisafulli and Hawkins 1998). Abundance of *Ascaphus* tadpoles in streams within the blast zone within five years of the disturbance was more than 90% of the herbivore biomass in some streams (Crisafulli and Hawkins 1998), and was at densities higher than had ever previously been reported for the area. Crisafulli and Hawkins (1998) speculated that colonists likely came from epicenters of survival within the blast zone rather than from more distant, unaffected populations. Snow-pack over many high-elevation streams may have acted as a buffer from the effects of the eruption, allowing some *Ascaphus* located in water or under snow to survive. Crisafulli and Hawkins (1998) believed that these individuals served as a source of colonists to streams at lower elevations where aquatic biota seemed to have been completely extirpated.

High water events (or freshets) above some magnitude are also destabilizing phenomena in reaches with sufficient fluvial power to entrain the substrate (this is typically outside of headwaters; see Brummer and Montgomery 2003). Metter (1968) showed that significant portions of entire annual cohorts could be removed by large magnitude high water events for populations now attributable to both *A. truei* and *A. montanus*. Though he did not track recovery from such events, he found adults post-event that could contribute to the relatively rapid recovery intervals reported by Hawkins and colleagues (1997; see previous paragraph). Similarly, Bury (1968) found a few *A. truei* in Graham's Gulch an unspecified amount of time after this second-growth Coast redwood forest stream had experienced major flooding linked to substantial reorganization during the major December 1964 storm in northern California.

Though unstudied, it may be possible for *A. truei* to select the most habitat stable portions of streams that represent a tradeoff between the headwaters regularly disturbed by mass wasting and downstream areas regularly disturbed by freshets with substantial fluvial power (see Brummer and Montgomery 2003 for discussion of the details of this tradeoff).

LITHOLOGY: Many lines of evidence suggest that tailed frog occurrence is linked to distinctive lithologies. Initially suggested on the basis of *A. truei* surveys in the Prince Rupert region of British Columbia (Dupuis and Friele 1996), Diller and Wallace (1999) provided the first formal assessment of this relationship in managed forests in northwestern California. Using a simple scheme that grouped lithology into consolidated and unconsolidated categories,[254] their analysis[255] identified lithology as the more important of two predictor variables. They recorded *A. truei* in 81% of 67 streams on consolidated lithologies, but not in the five streams having unconsolidated lithologies. Few streams on unconsolidated lithologies limit the strength of their conclusion. Dupuis and colleagues (2000) discussed the notion that lithology influences the character of stream substrates, but provided no formal analysis. Based on sampling 40 streams in southwest Washington, Wilkins and Peterson (2000) found *A. truei* in three of 22 streams on basalt lithologies, but none of the 18 streams on marine sedimentary lithologies. In this case, the low occupancy rate on basalt lithologies limited the strength with which they could withdraw a conclusion about lithological control on *A. truei* occurrence. In a broader analysis that encompassed then available data (see footnote 215) for British Columbia, Sutherland and Bunnell (2001; see also Sutherland 2000) found lithology to be the dominant predictor of *A. truei* occurrence. Employing CART analyses, they found that lithology explained 21.1% of the original deviance, more than twice the variation attributable to next most important variables explaining *A. truei* occurrence. In particular, intrusive or metamorphic bedrock formations better explained *A. truei* occurrence than any other single variable. Sutherland and Bunnell (2001) also identified lithology as a key predictor of *A. truei* density (22.5% of the original deviance), though in this case, it had less predictive ability than the clast size distribution of the stream substrate (37.0% of the original deviance). In seeming contrast to previous studies, Adams and Bury (2002) found similar patterns of occupancy for *A. truei* between lithologies that they considered consolidated versus unconsolidated over a broad area in Olympic National Park. In particular, they recorded *A. truei* at six of nine sites (67%) on consolidated lithologies and at 86 of 154 sites (56%) on unconsolidated ones. These data imply that lithological control on *A. truei* occurrence is unlikely (*contra* Kroll *et al.* [2008], who indicated that Adams and Bury [2002] found a positively relationship with consolidated geology), but this ignores several issues: 1) the number of sample sites on consolidated lithologies are too small from which to draw any confident conclusion; 2) their consolidated lithology category includes a broad range of distinct sedimentary lithologies, some of which are large-clast generating and to which *A. truei* response is likely to differ (e.g., in contrast, Wilkins and Peterson [2000] selected from one narrow category of marine sedimentaries; N. Wilkins, P. Peterson, 2011, *pers. comm.*); and 3) detectability varying among lithologies could change the conclusion regarding a relationship with lithology. Lithology is also tied to the quality (reflecting the size and competence) of substrates. Massive competent rock types, such as granites and intrusive basalts, generally produce coarser substrates that are suitable habitats, whereas fractured or brittle rock types, such as many sedimentaries lithologies produce abundant fine material smaller than fine gravel, which

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[254] Diller and Wallace (1999) grouped the 13 geological formations within their study area into two categories, consolidated and unconsolidated, based on formation age and particle type formed following decomposition. The consolidated category consisted of older formations that form coarse substrates (boulders, cobbles, and gravels) during decomposition into fine sediments, whereas the unconsolidated category included younger marine deposits that decompose directly into silt and sand.

[255] Diller and Wallace (1999) used a stepwise logistic regression to analyze 5 landscape-level variables from 72 randomly selected streams. Besides lithology (described by Diller and Wallace [1999] as geologic formation), forest age of the stand adjacent to each stream, stream aspect, elevation and cover type were analyzed. Cover types were grouped into redwood, Douglas-fir, redwood/Douglas fir mix, and hardwoods.

is thought to represent suboptimal habitat (Dupuis and Friele 1996, Dupuis *et al.* 2000, Wilkins and Peterson 2000).

Lithology has not been examined in ways potentially useful in predicting the distribution of *A. montanus.*

TOPOGRAPHY: In the Olympic Peninsula of Washington, Adams and Bury (2000, 2002) found a significant positive relationship between the abundance of *A. truei* and elevation (though the species occurred most frequently in mid-elevation streams), and a significant negative relationship between abundance and aspects deviating from north. Sutherland and Bunnell (2001; see also Sutherland 2000) found that for both occurrence and density of *A. truei*, topography (a composite variable that encompassed elevation, aspect and stream gradient) accounted for 9.5% and 11.1%, respectively, of the original deviance in an analysis of 22 habitat variables measured across sites in coastal British Columbia. However, unambiguous relationships between *A. truei* responses and each of these variables could not be identified.

Sutherland and Bunnell (2001; see also Sutherland 2000) also found that the same aforementioned topography variable explained little of the occurrence and abundance of *A. montanus* over its Canadian range. In particular, topography explained 3.3% and 9.9% of the original deviance in an analysis parallel to that done for *A. truei*.

POTENTIAL EFFECTS OF FORESTRY PRACTICES

Glenn Sutherland, Linda Dupuis, Marc Hayes, and Tanya Wahbe

The Early Years (1920-1979): Forestry practices affecting tailed frogs has its roots in comments dating from Gaige (1920) based on observations from near Lake Cushman (Washington). Referring to her study area on the east side of the Olympic Peninsula,[256] she stated that *A. truei* was "…found only in streams with densely forested banks with one exception." That exception was where she recorded the species in a small snow-fed creek running through a small alpine meadow on Mount Steel (1,372 m [4,500 ft]). Having established that *A. truei* was typically found along forested streams, she then commented on its occurrence in a harvested area along Laundry Creek, stating "The banks of Laundry Creek, flowing into Lake Cushman, had been recently logged for some distance and no adults were taken on this cleared slope, though several were captured just above it." Gaige made no comment about temperature conditions in the harvested versus unharvested areas of Laundry Creek, but a difference in habitat conditions was implied when she added: "A low temperature and cold water are evidently necessary for the welfare of the species, for they died very quickly when placed in the sunlight." One would think that this statement was not intended to implicate sunlight *per se* as the cause of mortality.[257] Given that Gaige was a careful investigator,[258] the basis of her rapid

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[256] Gaige (1920) conducted her work in the area from MacTaggert Creek (Mason County) in the south to creeks 40 km (25 mi) to the north on Mount Steel (Jefferson County) over an elevation range of 122 m to 1,372 m (400 ft to 4,500 ft).

[257] Gaige (1920) also commented that the larvae, "They seldom survived the trip home in a bottle, they would attach themselves to the glass above water and were usually dead in an hour or so."

[258] In a synoptic biography of Gaige, Ruthven (1936) stated, "Her careful work and sound judgment are well known…".

mortality comments are impossible to interpret without more context about the conditions under which she made those observations.

The second assumption Gaige (1920) made, which Noble and Putnam (1931) later stated more explicitly when discussing the same area, was that, "*Ascaphus truei* appears to be uniformly distributed throughout the area under consideration." The actual intent of this statement was to imply that *A. truei* was not visibly less common anywhere in this landscape *in the absence of timber harvest*. To this point, Noble and Putnam (1931) repeated the idea that *A. truei* was associated with forest, but in a slightly different way, stating, "At elevations from 200 ft to 3500 ft [61 m to 1,067 m] above sea level, adults and larvae appear to be confined to streams surrounded by forest." The elevation range restriction that this statement may seem to imply was probably unintentional, but it was followed by a statement that was intended to convey an unambiguous link between timber harvest and elevated temperature, stating, "Removal of the timber by lumbering or by fire results in the disappearance of *Ascaphus* apparently on account of the increased temperature of the exposed streambed." This statement was not simply an augmented cast of the observations of Gaige (1920) at Laundry Creek, as Gaige and Noble corresponded on the issue of harvest (*in litt*., Noble to Gaige, 1930). Noble, perhaps the prominent experimentalist of his time, did not provide data on increased temperature in exposed streambeds (relative to unexposed ones) or *Ascaphus* disappearance (in any sites pre- versus post-harvest).

Statements regarding the disappearance of *A. truei* in relation to harvested landscapes that originated from Gaige (1920) and Noble and Putnam (1931) were subsequently repeated or elaborated in uncritical fashion. Discussing a Coastal tailed frog-occupied stream north of Dyerville (Humboldt County), California, Myers (1943) ominously foreboded that, “Lumbering operations, which affect water temperature in such creeks, steadily approach the privately owned area in which *Ascaphus* Creek is located,…”. He followed this with the prediction that, “…and this southernmost locality for *Ascaphus*[259] may not long exist, unless it is soon added to...nearby state-owned [redwood] groves.” Later, Nussbaum and colleagues (1983) stated that, “Tailed frogs disappear from streams within logged areas.” To their credit, they also proposed that, “In view of the extensive logging that continues to occur throughout much of their range, the exact effects of logging on populations should be studied.” Bias regarding whether timber harvested landscapes were even occupied is suggested in literature as late as the 1990s. For example, Adams and Wilson (1993), in their report addressing the first record of *A. truei* for the Willapa Hills, stated "…on the tributary where the [tailed] frog was collected there is a stream buffer zone (ca. 100 m on each side) and much of the timber in its surrounding headwaters is uncut. These factors may preserve populations." Their statement implies that *A. truei* might not have been found at the location in the absence of significant unharvested area.

Metter (1964*a*) was the first to provide an observation on a pre- versus post-harvest contrast for any tailed frog. He stated that, "A creek 1.5 miles [2.4 km] downstream from…[his] study site held a number of *Ascaphus* until the area was logged in 1960, after which the animals disappeared."

Despite these statements about disappearance, recognition emerged relatively early that the effects of forestry practices might vary geographically. Bury (1968) mentioned that

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[259] This location was the southernmost known for *A. truei* at the time Myers (1943) wrote this paper.

harvest may eliminate suitable conditions for tailed frogs in some streams, but noted that the occurrence of *A. truei* in Pine Creek, Railroad Creek, the tributaries of Redwood Creek and Graham's Gulch, all areas managed for timber harvest in coastal Humboldt County (California), suggests that harvest is less detrimental to tailed frogs in a maritime climate. This idea was not explicitly examined until 30 years later.

The Era of Implemented Studies (1980-1994): Concern for the rapid disappearance of old-growth stands, primarily on federal lands in the United States during the 1980s and early 1990s, led to subtle changes in the arguments about tailed frog habitat requirements. The notion that tailed frogs vanish after harvest was replaced with old-growth forest structure as the requirement for their maintenance and survival in forested landscapes (see Welsh 1990, 1993). This approach may have been taken at least in part to leverage support for the preservation of old-growth stands, a situation in which economics and politics often trumped science in polarized arguments. Consequently, a number of earlier studies were focused on old-growth/harvested stand contrasts, some of which were designed to determine the degree of associations between old-growth and different taxon groups, among them amphibians. Tailed frogs were prominent among the species of interest. These efforts were important in ultimately spurring studies that would enhance understanding of the forestry practices/stream-associated amphibian relationship.

Though not addressing tailed frogs, selected earlier old-growth/harvested stand contrast studies provided important perspectives about processes in streams that may harbor tailed frogs. Aho (1976) was the first to draw attention to the fact that animal responses to forestry practices might be complex. He found abundance of Cutthroat Trout in a western Oregon Cascade stream flowing through a small clear-cut harvest unit greater than in the adjacent upstream reach through undisturbed forest.[260] This result appeared to contradict earlier studies in the Oregon Coast Range that revealed that clear-cut harvests led to declines of Cutthroat Trout (Hall and Lantz 1969; Moring and Lantz 1974, 1975). This apparent contradiction led Murphy and Hall (1981) to re-examine Aho's result to try to identify its cause. Murphy and Hall (1981) measured the response of the aquatic predator assemblage because they thought it would best integrate the total trophic response.[261] Murphy and Hall (1981) conducted a retrospective study[262] on 15 old-growth, 10 clear-cut, and six second-growth sites in the McKenzie River drainage on or near the H. J. Andrews Experimental Forest.[263] To detect harvest impacts that might vary with stream size or gradient, they compared nine pairs of adjacent clear-cut and old-growth sites on

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[260] Aho (1976) conducted a mark-recapture study of Cutthroat Trout on two 200-m (one harvested and the other unharvested) sections of the same stream.

[261] Murphy and Hall (1981) selected aquatic predators for which they felt abundance could be quantified: fishes, salamanders, and aquatic life stages of Coleoptera (beetles), Megaloptera (dobsonflies), Plecoptera (stoneflies), Odonata (damselflies and dragonflies), and most Trichoptera (caddisflies) in the genus *Rhyacophila*. Predatory aquatic Diptera (flies) and terrestrial vertebrates that search for prey in streams (e.g., American Dipper) were not sampled.

[262] No data were available on preharvest conditions, so Murphy and Hall (1981) assumed that on average, no difference existed between sites before harvest.

[263] Old-growth sites were undisturbed by harvest but clear-cuts were sometimes present 1-2 km upstream. Harvested sites had been clear-cut without buffers and later burned. Murphy and Hall (1981) divided harvested sites into two groups based on their vegetation structure: clear-cut (5-17 years post-harvest) with streams remaining mostly unshaded, and second-growth (12-35 post-harvest) with heavy shaded by deciduous vegetation. Old-growth sites were partially exposed to sunlight due to fallen trees. Old-growth and clear-cut sites were selected to provide a broad range of drainage area; stream width, depth, and gradient; and elevation. Second-growth sites were located at lower elevations because of the historical pattern of harvest regionally.

streams differing in size (based on Strahler [1952] stream order) and gradient. Clear-cut/second-growth contrasts were used to assess post-harvest succession. Recapture and removal approaches by electrosampling a 30-m reach at each site[264] was the vertebrate sampling approach; insects were removal-sampled with a kicknet. For the paired site contrast, species richness and total biomass of predatory insects averaged 28% and 88% greater, respectively, in clear-cut than in old-growth sites. However, insect density; and vertebrate species richness, biomass, and density did not differ between clear-cut and old-growth sites. Ten species of vertebrates were recorded across the 31 study sites, but the Coastal Giant Salamander dominated in both biomass and frequency of occurrence, making up to 99% of the total predator biomass at selected sites. Evaluating the 10 most common taxa (Coastal Giant Salamander, Cutthroat Trout, and eight species of insects), biomass was significantly greater in clear-cut than in old-growth sites for Cutthroat Trout and three of the insect species. No overall differences were found for the Coastal Giant Salamander and remaining insect taxa, but clear-cut harvest effects seemed to be gradient-dependent for the salamander. In particular, the percentage difference between clear-cut and old-growth sites was strongly correlated with gradient ($r_s = 0.83$, $P < 0.01$), which tracked the percentage difference in substrate crevice density between site categories ($r_s = 0.78$, $P < 0.05$). Namely, salamander biomass became progressively greater in clear-cut sites versus old-growth sites for gradients over 9%, but that difference was reversed and became greater in the reverse direction at gradients ≤9%. Further, chlorophyll accumulation in clear-cut sites was greater than in adjacent old-growth sites ($P < 0.05$). Thus, clear-cutting seemed to enhance periphyton production by canopy removal, but this effect was reduced in typically more open larger streams.

From a historical perspective, the Murphy and Hall (1981) study was important in two ways. First, it established that timber harvest effects were complex with both positive and negative consequences, even at a regional scale. Second, the study provided the first basis for understanding how harvest effects might shift. In particular, higher gradients seemed to attenuate negative effects attributable to sedimentation. This study made it important to consider gradient impacts on harvest effects in different landscapes as well as considering gradient in study designs attempting to better understand those effects.

A second study, also done in western Oregon (Murphy et al. 1981), examined three pairs of coarse versus fine sediment-dominated streams at three intervals in succession (recent clear-cut, second-growth, and old-growth).[265] This study found that streams traversing recent clear-cuts generally had greater rates of microbial respiration, and greater densities or biomasses of aufwuchs, benthos, drift, salamanders, and trout than did shaded, forested sites regardless of sediment composition. Murphy and colleagues (1981) concluded that shifts in trophic status and increased primary productivity due to shade removal in these streams may mask the effects of sedimentation.

Generalization from the above study was difficult in part because study streams were limited in fine sediments (0-30% sand <1 mm or smaller) and stream power was low. This led to the follow-up study (Hawkins et al. 1983) that included more streams,

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[264] The recapture pass was typically done one week after marking.

[265] Murphy and colleagues (1981) used coarse- versus fine-dominated streams, respectively, with 56-76% cobble versus 5-14% sand and 23-53% gravel. Recent clearcut, second-growth and old-growth successional categories were, respectively, 5-10 years post-harvest; 30-40 years post-harvest; and >450 years old. The second-growth category was deciduous canopy-dominated whereas the old-growth category was conifer-dominated.

including those with greater levels of fines (up to 80%). Hawkins and colleagues (1983) measured riparian canopy,[266] physical habitat,[267] and the density of fishes (salmonids and sculpins) and Coastal Giant Salamanders[268] in 10 pairs of streams with high versus low levels of shading.[269] They found fishes more abundant in streams with high levels of shade than in streams with limited shade, but salamander abundance seemed unrelated to shading. Salamander and sculpin densities were associated with substrate composition; salamanders were found only at high-gradient sites with largely coarse substrates (<30% sand); sculpins were most abundant at lower-gradient sites with finer-sized sediments. In contrast, salmonid abundance was only weakly associated with substrate type. The focal finding in this study was the interaction between canopy and substrate on the density of total vertebrates and invertebrates. In particular, densities decreased as the percentage of fine sediment increased among shaded streams, but no such relationship was evident in the open (low shade) streams. The mechanism was thought to be that greater sunlight increases stream primary production that can masks the negative effects of greater levels of fine sediment. Though this study did not address tailed frogs, it suggested a way in which tailed frog response might vary with different levels of sediment and shading.

Among the earliest clear-cut versus old-growth studies was a retrospective comparison of harvested and old-growth redwood forests done in northwestern California (Bury 1983). Four paired 20 m × 50 m plots (one harvested and one old-growth plot per pair) were selected on the basis of similarity in slope, aspect, and vegetation. The harvested plot in each pair was located in stands harvested 6-15 years earlier. Over the mid-January-early February period, surveyors sampled paired plots consecutively to minimize weather-related bias. Plots were searched for amphibians by turning surface debris and small logs (<0.5 m dia) and raking litter. Species richness in harvested plots ($\bar{x}$ = 3.3, range: 2-4) did not differ from old-growth plots ($\bar{x}$ = 3.5, range: 3-6), but plot types were described as being distinctly qualitatively different because some species were recorded only in the old-growth plots whereas others were found exclusively in harvested plots. However, low counts of individuals render these differences ambiguous. For example, part of this difference[270] was based on the fact that one post-metamorphic *A. truei* was found in a

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[266] Hawkins and colleagues (1983) measured riparian shading of the streambed measured with an angular canopy densiometer during sampling. Ten points were taken and averaged in each stream section and for each reach.

[267] Hawkins and colleagues (1983) measured surficial sediments from core samples taken in triplicate from each of riffles and pools. A 0.25-m^2 metal core was driven into the stream bed and 10-15 L of substrate were removed. Particles were wet-sieved into <0.05 mm, 0.05-1 mm, 2-4 mm, 5-16 mm, 17-50 mm, and >50 mm size classes. Percent composition was calculated based on volume after organic matter was removed either by hand or combustion (550°C, 24 h). Hawkins and colleagues (1983) also estimated stream stability based on Pfankuch (1975).

[268] Hawkins and colleagues (1983) recorded 13 instream vertebrate species, but only three salmonids (Rainbow Trout [*Oncorhynchus mykiss* (as *Salmo gairdneri*)]; Cutthroat Trout, and Coho Salmon [*Oncorhynchus kisutch*]), three sculpins (Reticulate Sculpin [*Cottus perplexus*], Prickly Sculpin [*C. asper*], and Coastrange Sculpin [*C. aleuticus*]), and the Coastal Giant Salamander (*Dicamptodon tenebrosus* [as *D. ensatus*]) were considered in analysis. All other vertebrate species made up ≤10% of instream vertebrates. For analysis, salmonid and sculpin taxa were combined.

[269] Canopy shaded 67-90% of one stream in each pair, whereas the other stream in each pair had little or no shade (0-23%).

[270] The rest of this difference was that two larval Southern Torrent Salamanders (*Rhyacotriton variegatus* given as *R. olympicus*) and three larval Coastal Giant Salamanders (*D. tenebrosus* given as *D. ensatus*) were found in the same rivulet of the same plot as the *A. truei* and one juvenile Coastal Giant Salamander was also found in the same plot; one Del Norte Salamander (*Plethodon elongatus*) was in a second old-growth plot; two juvenile Coastal Giant Salamanders were in a third old-growth plot; one Pacific Treefrog (*Pseudacris regilla* given as *Hyla regilla*) was in a harvested plot; and two Northwestern Salamanders (*Ambystoma gracile*) were in a second harvested plot. All

rivulet on one of the harvested plots, whereas none were found in the searches of logged plots. Even ignoring the low numbers of amphibians found, this study lacked sufficient power to interpret contrasts between harvested and old-growth plots.

Hawkins and colleagues (1988) provided the first study with substantial perspective on the landscape features influencing *A. truei* abundance with analogs in forestry practices. They examined 8-13 streams in each of three years near Mt. St. Helens that differed in level of disturbance sustained during the 1980 eruption and were categorized as having either forest over the entire basin, forest only in the headwaters, or no forest.[271] Differences in density of *A. truei* among streams were most clearly associated with the extent of forest in individual basins, whereas within-stream density differences reflected substrate size, embeddedness, and current velocity. Hawkins and colleagues (1988) found that streams in basins with little forest had temperature maxima near 20°C and few *A. truei*; and also noted that in at least partly forested basins, temperature maxima were <18°C, and larval densities were relatively high. However, they also commented that lack of correlation between larval density and water temperatures was inconsistent with the interpretation that low larval densities in the no forest sites were a function of high temperatures. Still, Hawkins and colleagues (1988) were cautious about dismissing temperature as potentially limiting since they had measured it exclusively in the lower reaches of each basin. They noted that post-eruption conditions are similar to those in streams after clear-cut harvest. This study's value in understanding effects that might result from forestry practices was in its identification of environmental changes that might persist, namely, embeddedness of stream substrates due to sedimentation. This and temperature became foci in later studies attempting to understand the potential effects of forestry practices. Despite being a well-executed design (for its time), this study also illustrates the difficulty that retrospective and correlative studies have in disentangling reasonable alternative hypotheses. In this case, difficulty arises from the facts that pre-eruption data on sedimentation and temperature from study streams was lacking.

In work done on the H.J. Andrews and Wind River Experimental Forests in Oregon and Washington, respectively, Bury and Corn (1988*a*) introduced pitfall trap array sampling (Bury and Corn 1987) for evaluating differences between 30 forest stands. In comparison across a three-category chronosequence (young second-growth, mature, and old-growth),[272] Bury and Corn (1988a) found no significant difference in *A. truei* captures among the categories,[273] though they noted that, "...the mean abundance of common species [among them *A. truei*] appeared to differ across...[the] forest development... gradient." This statement is risky because Bury and Corn (1987) had stated that estimates of population density could not be made with pitfall trapping without some separate line

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species were found only in the plot types (harvested or old-growth) indicated.

[271] Sites with no forest (six watersheds) had the entire forest blown down and all vegetation killed, sites with headwater forests (three watersheds) had forests in the lower basins destroyed, but trees in the upper 30-50% of the basins were not killed, and forested sites (four watersheds) received heavy ash fall, but the vegetation was not destroyed. All watersheds were similar in size (5-10 km^2 drainage area) and average slope (15-20%). The number of watersheds sampled varied each year because of time constraints and seasonal access to sites.

[272] In their chronosequence, Bury and Corn (1988a) used the following intervals: clear-cut sites (<10 years since harvest), young second-growth (30-76 years old), mature (105-150 years old), and old-growth (195-450 years old).

[273] Bury and Corn (1988a) had four chronosequence categories (clear cuts were the fourth category), but they tested for differences among three (young second-growth through old-growth) using the log-transformed capture data in a one-way ANOVA. For *A. truei*, the result was $F_{df(2,14)} = 0.92$, $P = 0.42$.

of assessment due to inability to define the areas effectively trapped. The pitfall approach of Bury and Corn (1987) is useful to evaluate phenology, but its value as a tool to assess relative abundance over a forest chronosequence (Bury and Corn 1988a) is questionable.

In the same year, Bury and Corn (1988*b*) reviewed available information on responses of stream-associated amphibians to forestry practices. They pointed out that the immediate effects of clear-cut harvest on amphibians other than Coastal Giant Salamanders[274] was poorly studied, so a large part of their review addressed what they considered as likely physical effects of harvest on the biological requirements of stream-associated amphibians. In their review, Bury and Corn (1988*b*) partitioned effects into short- and long-term based on the perceived differences in a timeline for recovery for those effects. They addressed two effects as short-term: alterations in temperature and food resources. Both were considered short-term because re-establishment of canopy that could restore pre-harvest conditions for these factors was viewed as relatively rapid.[275] They expected that the consequences of increased temperature for *A. truei* were likely to be negative because increases in water temperatures following harvest were sometimes large (Brown and Krygier 1970) and the temperature requirements of embryos (Brown 1975) and temperature selection patterns of larvae (de Vlaming and Bury 1970) were both low (≤19ºC). This suggestion has to be viewed in the historical context of available data because Brown and Krygier (1970) recorded large increases in water temperatures where an entire basin was clearcut. Bury and Corn (1988*b*) thought that alteration of food resources was a possible short-term effect of clear-cut harvest because *A. truei* larvae rely almost entirely on diatoms (Altig and Brodie 1972), and a shift away from diatoms (toward filamentous green algae) can occur with increased sunlight and/or stream temperatures (Beschta et al. 1987). This kind of shift was thought to have the potential to limit or eliminate food for larvae. To illustrate the long-term effects of timber harvest, Bury and Corn (1998b) first introduced some results of their long-study addressing those effects, published the following year (Corn and Bury (1989). They considered the long-term effect of harvest to be alteration of stream habitat, of which sedimentation was focal. Their long-term study was retrospective and conducted in central western Oregon. Corn and Bury (1989) compared the occurrence and abundance of four stream-associated amphibian species (including *A. truei*) in 23 streams flowing through old-growth forests to 20 streams flowing through 14-to-40-year-old second-growth. They found species richness and the density and biomass of all four species significantly greater in streams in old-growth than in second-growth. Physical characteristics of streams in old- and second-growth streams were similar except that second-growth streams generally had finer substrates, which they interpreted as resulting from greater sedimentation. *Ascaphus truei* occurred more often in streams in harvested stands when uncut timber was present upstream, but neither density nor biomass of any species were related to either presence of uncut timber upstream or years since harvest. Bury and Corn (1988*b*) believed that the effects of sedimentation would vary geographically and with gradients, being more severe in those areas of the PNW having lower levels of precipitation (lower latitudes and

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[274] Specified as Pacific Giant Salamander, the old name, in their review.

[275] Bury and Corn (1998*b*) based their assessment of rapid recovery on Andrus and Froehlich (1988), who indicated that recovery of stream shading is rapid, can reach 50 percent in less than 5 years and pre-harvest levels after 10 years in the Oregon Coast Range. This view substantially underestimates the current view of shading recovery patterns post-harvest, which rarely even reaches three years, largely due to stream shading by shrubs.

more interior locations) and where lower gradients existed (mostly lower elevations). These patterns led Bury and Corn (1988*b*) to develop conceptual models that characterized post-harvest response for stream-associated amphibians. The conceptual model for *A. truei* hypothesized that in places where sedimentation effects were severe, the species would be locally extirpated (that is, extirpation occurred within the drainage basin, presumably requiring recolonization from outside the basin). In regions where sedimentation was limited, *A. truei* would survive, but population levels would recover only slowly (on a multi-decadal scale) in concert with the recovery of substrate conditions that provided suitable habitat. The conceptual models that Bury and Corn (1988*b*) developed had particular value in that they provided testable hypotheses for future studies.

Related to the earlier-mentioned debate about preservation of old-growth, Welsh (1990) presented work on three forest-associated amphibians (among them *A. truei*)[276] that had been most frequently detected in mature or old-growth stands in northwestern California and southwestern Oregon. This work was part of US Forest Service efforts dating from 1981 that focused on identifying which vertebrate species require old-growth. Welsh (1990) found that *A. truei* occupied a progressively greater proportion sites with greater stand age (see footnote 26) but not greater tailed frog density at least across the full dataset. However, Welsh argued that because his high-elevation sites[277] differed based on forest type (i.e., they were true fir [*Abies* spp.]-dominated), they should be removed from an analysis of lower-elevation sites. Examining only the 26 lower-elevation sites using stand age as a continuous variable, he found a positive relationship between *A. truei* density and stand age (r^2_{adj} = 0.29, P = 0.003). The relationships between forest age and occurrence or abundance that Welsh (1990) proposes should be viewed cautiously. Welsh does not provide an explanation on how he selected sites at the landscape (study) level (see p. 17), which limits the ability to understand the population of forested sites to which his conclusion can be generalized. Furthermore, the study had a low sample size of young forest sites, which makes the selection of those sites critical to understanding the strength of relationship. Additionally, examination of the reduced dataset suggests that the relationship may have been driven by the two highest density points that both occurred in old-growth (see Welsh 1990; his figure 3c). Even if valid, the relatively low co-efficient of determination for the density-forest age relationship indicates that something other than forest age explains most variation in *A. truei* density. Interestingly, Welsh (1990) believed that the lack of a strong relationship to forest age reflected the fact that it is an indirect measure of the factors limiting *A. truei*, and postulated that aspects of

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[276] The Olympic Salamander, *Rhyacotriton olympicus* (= Southern Torrent Salamander, *R. variegatus*) and the Del Norte Salamander were the remaining two species (Welsh 1990). Welsh collected data over the interval 1984-1986 using three sampling methods: pitfall traps, time-constrained terrestrial searches, and area-constrained aquatic searches, but only area-constrained aquatic searches yielded enough *A. truei* captures for analysis. Aquatic searches were conducted at 39 first- or second-order streams in July-August 1984-1985. Streams were categorized as flowing through young (60 ± 18 SD years old; *n* = 9), mature (147 ± 30 SD years old; *n* = 9), or old-growth (344 ± 86 SD years old; *n* = 21) forest stands. Selection procedure for these 39 sites within the larger landscape was unexplained, so whether it was random is unclear (Kroll 2009). Welsh (1990) selected three 5 m reaches 1-3 m wide, each spaced by 50 m; the first reach was selected 50 m upstream from the nearest trail or road access. Reaches were searched in a single pass, moving all rocks where possible, working upstream with catch nets placed downstream to capture dislodged animals.

[277] Welsh (1990) considered his high-elevation sites those 1000 m (3,281 ft) or higher in elevation. Thirteen of the 39 sites he examined using aquatic searches fell into this category.

microclimate or microhabitat are likely the limiting factors. Ironically, this belief argues that forest age is important only insofar as those aspects of microclimate or microhabitat crucial to tailed frog exist, which as the data of Welsh (1990) show, were only manifest in his study at low elevations in northwestern California and southwestern Oregon and in a way that has only moderate explanatory power. Suffice it to say that the ambiguities in the data of Welsh (1990) complicate interpretation. Ambiguities notwithstanding, the importance of the work of Welsh (1990) was to identify the possibility that *A. truei* is more vulnerable to extirpation in early seral habitats toward the California end of its geographic range.

In the early 1990s, a suite of studies focused on old-growth in comparison to a range of other forest age classes in Oregon (Corn and Bury 1991, Gilbert and Allwine 1991) and Washington (Aubry and Hall 1991, Bury and colleagues 1991*b*) supported the suggestion of Welsh (1990) that microclimate or microhabitat were limiting *A. truei*. Collectively, these studies revealed that moisture was important, and that moisture conditions varied across forest types as a function of latitude. For example, on the west Cascade slope in Oregon, Gilbert and Allwine (1991) found *A. truei* frequently in young forests and infrequently in old-growth on the Mt. Hood National Forest, but the reverse pattern existed on the Umpqua National Forest to the south. The infrequency of *A. truei* in old-growth on the Mt. Hood National Forest also suggests that some factor other than moisture is limiting. All these studies used pitfall trapping (see Bury and Corn 1987), so interpreting relative occurrence and abundance patterns must be done with caution.

The Era of Manipulative Studies (1992-present): In a series of three modest experimental studies conducted near Mt. St. Helens, Washington in 1986 (see description under BIOTIC INTERACTIONS section on p. 86), Lamberti and colleagues (1992) ushered in a new era – the addition of manipulative studies to the approach palate for informing the potential effects of forestry practices on tailed frogs. This work did not involve a harvest treatment manipulation, but it did reveal that tailed frog larvae could reduce periphyton levels at higher densities, that site-specific variability could trump the potential grazing effects of *A. truei* larvae, and that grazing invertebrates could achieve periphyton reduction patterns similar to tailed frog larvae. This work provided some basis for understanding how tailed frogs might be limited when interpreting harvest treatment studies.

However, the first manipulative study that actually used harvest treatments was that of Kelsey (1995), who designed a modest landscape-scale study that examined the responses of stream amphibians to forest harvest as part of her dissertation. Conducted over the interval 1992-1994, this study was originally targeted nine potential harvest units in the mid-elevation landscape of the Green and Puyullap River in western Washington. In a BACI design (Smith 2002) with one year of pre- and two years of post-harvest sampling, six units were to be harvested between summer amphibian sampling in the pre-harvest year (1992) and equivalent sampling in the first year after harvest (1993); the remaining units were to be unharvested references. Complications arose from combination of road construction, the location of a northern spotted owl (*Strix occidentalis*) nest, and operational logistics that resulted in only four of the six sites being harvested between 1992 and 1993. Two more of the original sites were harvested between 1993 and 1994, but a fourth reference was also added, which could have broadened the study to 10 sites. However, further complications and an analysis constrained to comparing the logarithm of the pre- to post-harvest ratio of *A. truei* densities between 1992 and 1994 between harvest and reference units severely reduced units available for comparison in her final analysis. For *A. truei* larvae, analysis used three references and two harvest treatments, whereas for post-metamorphic *A. truei*, the analysis involved four references and two harvest treatments.[278] Moreover, one of the two treatments that could be used for comparison for larvae was not the same treatment that could be used for post-metamorphs. This effort was clearly reduced to a suite of case studies, but the larval comparison revealed a significant difference (*P* = 0.015); that for post-metamorphs did not (*P* = 0.957).[279] Kelsey (1995) concluded that the density of *A. larvae* increased significantly in reference sites relative to treatment sites, but though the effects of harvest were immediate, larval densities in treatment streams did not decrease dramatically. Kelsey (1995) also noted that the presence of 1st-year larvae in harvest units immediately post-harvest, which were not included in the analysis, indicated evidence of reproduction. Beyond the obviously small samples sizes, large inter-year and among-site variability in densities reflected by the ratio logarithms suggests caution in interpretation. Nonetheless, the value of this study was introducing a manipulative approach within a fundamental strong design that provided a useful template for further work.

Simultaneously, O'Connell and colleagues (2000) undertook a multi-dimensional, multi-taxon landscape-level study to examine potential forest practices effects over the period 1992-1998.[280] Kelsey (2000) authored the stream amphibian portion of this study, which included *A. truei* and involved 18 western Washington sites. In this study, Kelsey found no significant differences among treatments in post-harvest abundance of *A. truei* larvae (*P* = 0.854).[281] However, five of the 18 sites lacked stream-associated amphibians, which greatly reduced statistical power. As a consequence, Kelsey (2000) did a power analysis to estimate how many sites would have been needed to distinguish treatment effects; she obtained the figure of 100 sites. Whether this result arises from the intrinsically high variability of *A. truei* abundance data, a small effect size, or some combination thereof is unclear. The manipulative aspect of both these study was an improvement in approach, but execution limitations that arose in both studies resulted in the question of a forestry practices effect on *A. truei* remaining ambiguous.

In the Wallowa Mountains of northeastern Oregon, Bull and Carter (1996*a*) conducted the first study on *A. montanus* addressing the potential influence of forestry practices.

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[278] A key constraint on the number of units compared was that Kelsey (1995) only compared units where at least some 2nd-year larvae were present in at least one pre- or post-treatment year. This was done because of potential bias related to sampling occurring in different months between years that would miss 1st-year larvae.

[279] Comparison used a two-sample t-test (Kelsey 1995).

[280] This study, termed the Riparian Management Zone or RMZ study, involved 36 sites, half of which were in western Washington; the other half of which were in eastern Washington. Sites in each region were assigned to one of three treatments: 1) a reference unharvested for this study, but previously in the harvest rotation; 2) an application of the existing state buffer under Timber, Fish and Wildlife rules, which was retaining a 15 horizontal m (50 horizontal ft) buffer on both sides of each stream in the harvested stand; and 3) a state-modified buffer, which was a buffer of variable width, ranging from 7 horizontal m (25 horizontal ft) to 30.5 horizontal m (100 horizontal ft). In the state-modified buffer, the range of values represented extremes in possible buffer width, but the mean buffer width at any one site (treatment) was greater than the minimum value. In addition, though the mean widths in treatments were significant different between the existing state and state-modifier buffers, under- or over-application of the target widths resulted in an actual range of widths that differed from the intended targets. As a consequence, mean buffer width on state treatments ranged from 7.3 horizontal m (24 horizontal ft) to 23.2 horizontal m (76 horizontal ft), but state-modified treatments ranged from 20.6 horizontal m (68 horizontal ft) to 47.9 horizontal m (157 horizontal ft).

[281] Kelsey (1995) sampled amphibians by block-netting three 10-m stream reaches in each study stream in each sample year.

Their retrospective study compared 30 streams influenced by low, moderate, or high levels of timber harvest.[282] They found no significant differences in numbers of larvae or frogs in among treatments, though they commented that the average number of larvae and adults in streams declined with increasing harvest intensity.[283] Bull and Carter's (1996a) data were highly variable (co-efficients of variation uniformly >1). Even after reporting the values with highest (presumably outlier) stream numbers removed in each harvest category, co-efficients of variation remain above 1. Interestingly, Bull and Carter (1996*a*) noticed that stream characteristics seemed more important than landscape characteristics in predicting *A. montanus* abundance. The amount of cobble and fines best predicted larval abundance, whereas stream buffer presence, the amount of boulders and cobble and gradient best predicted adult abundance. Besides being the first study designed to address potential timber harvest effects on *A. montanus* (rather than simply comparing forest age classes), the Bull and Carter (1996a) study was the first of several after Welsh (1990) that suggested that stream characteristics supercede landscape characteristics (forest age) as an important control on occurrence or abundance of tailed frogs.

In a retrospective study done in southwestern British Columbia, Wahbe (1996; Wahbe and Bunnell 2001, 2003) examined 10 headwater streams· addressing three treatments: recent clear-cut, mature second growth, and old-growth.[284] Wahbe and Bunnell (2001) found a substantial difference in larval movements among treatments;[285] in particular, movement of *A. truei* larvae in streams in the old-growth treatment was significantly

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[282] Bull and Carter (1996a) classified streams with <20 percent of the landscape harvested as low, 21 to 50 percent as moderate, and >50 percent as high. They defined timber harvest as comprising clearcuts, shelterwood removals, overstory removals and partial overstory removals within the last 20 years. Determinations of the degree of timber harvest for placement into the aforementioned classes were made from a combination of aerial photographs, harvest records, and ground truthing. Streams selection was subjective based on: 1) timber harvest data, 2) accessibility (within 1 km of a road), 3) prior knowledge that *A. montanus* occurred in the watershed, and 4) presence of suitable habitat. Suitable habitat for *A. montanus* was defined as a perennial, cold stream with a cobble and boulder substrate. To reduce variability, they used only streams flowing through forested land and with gradients between 5 and 20 percent. Streams were sampled as close to the headwaters as feasible, so all streams sampled were less than 2 m wide and less than 0.5 m deep.

[283] Bull and Carter (1996a) surveyed a 1000-m of each stream for *A. montanus* using both diurnal and nocturnal searches. Diurnal searches were conducted between 25 May and 6 July 1993. A diurnal search consisted of walking upstream, overturning rocks, and holding a dip net downstream from the rocks to capture *A. montanus* life stages. Each stream was searched for 8 staff-hours. Only larvae were captured during the diurnal search. The same 1000-m of each stream was surveyed at night for 8 hours between 1 June and 1 July 1993. During the nocturnal search, a surveyor walked along the stream edge looking for adults (adults was used loosely in this study to mean any post-metamorphic individuals) in the water and along the shore. They reported an average number of larvae per 1000 m survey (standard deviation in parentheses) for the 10 streams in each of the low, moderate, and high harvest categories, respectively, as 162 (287), 88 (124), and 101 (251); the same data for adults was 35 (42), 29 (32), 23 (36). Because the highest larval and adult counts in each harvest category tended to be high, they also reported means (and standard deviations) with the stream with highest value in each category deleted; for larvae, in the same respective order, those figures were 75 (87), 58 (85), and 22 (24); for adults, the figures were 26 (33), 24 (32), and 13 (15).

[284] Wahbe (1996) used three watersheds (Elaho, Squamish, and Mamquam watersheds) to replicate her recent clear-cut (<5 yrs old), mature second-growth (60-80 yrs old), and old-growth (250+ yrs old) treatments three times. In addition, a tenth stream with a clear-cut and 50-m old-growth two-sided riparian buffer in the Ashlu watershed was used, but not replicated. Streams were selected based on presence of *A. truei* larvae and lacked resident game or anadromous fish, and except Ashlu, Elaho and Mamquam clearcut sites were chosen upstream from logging roads.

[285] Wahbe and Bunnell (2001) replace a clearcut site due to loss of access, which obscured their efforts to document a watershed effect using a General Linear Model. Nevertheless, distances moved differed significantly among treatments. They recorded *A. truei* larvae moving an average of 0.15 m/dy ± 0.02 m/dy SD m in clearcuts (n = 15), 0.28 m/dy ± 0.10 m/dy SD m in second-growth (n = 18), and 1.11 m/dy ± 0.30 m/dy SD m in old-growth (n = 22). A Duncan's multiple range test confirmed that movements in old-growth streams were greater than movements in clearcut or second-growth streams.

greater than movements in streams surrounded by clearcuts or second growth. Movement rates were more associated with amount of debris (logjams) than other measured parameters (gradient, stream width, pH, stream temperature, canopy cover). Wahbe and Bunnell (2001) suggested two hypotheses to explain their findings: 1) more debris (or logjams) may impede movement of larvae in recently harvested sites, or 2) more food through increased productivity in exposed sites may reduce their need to move. Since recapture frequency was low, how unrecognized movements greater than the relatively small study footprint influences study interpretation is unclear. Testing these hypotheses will require examination of larval movement among these forest types at a larger spatial scale using an approach that addresses potential differences in detectability. Wahbe and Bunnell (2001) found no significant differences in any of the larval variables measured (density, biomass per unit area, mean mass or mean length; $P > 0.182$ in all cases) among treatments, but power was low.[286] Larval biomass per unit area was low where silt was present.[287] Higher larval *A. truei* biomass per unit area and density were also associated with increasing elevation, decreasing stream size and a decreasing proportion of riffles relative to other reach types. Wahbe and Bunnell (2001) concluded that aspects of microhabitat and site parameters seem to strongly alter larval response. They recognized that they could not determine whether differences in larval biomass and density were due to forest treatment alone because their study streams did not flow through continuous patches of old-growth, second-growth and clearcut sites. And as in their movement study, detectability was not addressed. Wahbe and Bunnell's (2001, 2003) studies identified movement as a useful metric, and reinforced, by implication, the original idea of Welsh (1990) that microhabitat and site variables (as opposed to forest age) may be the key controls on *A. truei* populations.

In a brief review, Richardson and Neill (1998) summarized patterns among stream-associated amphibians in managed landscapes. Their review was based on having evaluated stream-associated amphibian populations across 144 sites in forests at different stages of succession in southwestern British Columbia.[288] They made the *a priori* prediction that if harvests lead to reductions in population sizes for stream-associated amphibians, a greater chance of extirpation is anticipated in harvested versus unharvested areas. They further reasoned that greater chance of local extirpation should translate into less frequent occurrence. However, Richardson and Neill (1998) found no significant differences in the occurrence of *A. truei* larvae as a function of surrounding forest age.[289] They also recorded no difference in larval densities between clearcut and old-growth sites, but the average mass of *A. truei* larvae was lower in clearcut than in old-growth

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[286] Wahbe and Bunnell (2003) reported power (1-ß) ranging from 0.150 to 0.330. Density (numbers/m^2) in old-growth (1.29 ± 0.20 SD) averaged 1.9 times that in second-growth (0.67 ± 0.17 SD) and 1.6 times that in clearcuts (0.67 ± 0.17 SD). Biomass per unit area (g/m^2) in old-growth averaged 0.53 ± 0.05 SD, 0.30 ± 0.07 SD in second-growth, and 0.47 ± 0.05 SD in clearcuts. Mass (g) of larvae averaged 0.46 ± 0.04 SD in old-growth, 0.41 ± 0.03 SD in second-growth, and 0.50 ± 0.05 SD in clearcuts. Length (as snout-vent length in mm) of larvae averaged 12.36 ± 0.27 SD in old-growth, 11.53 ± 0.20 SD in second-growth, and 11.98 ± 0.28 SD in clearcuts.

[287] Wahbe and Bunnell (2003) found larval biomass averaged 0.18 ± 0.03 g/m^2 where silt was present and 0.60 ± 0.14 g/m2 where silt was not present ($t = 2.603$, $P = 0.035$, $n = 9$).

[288] Richardson and Neill (1998) based their review on work done in the Chilliwack and Skagit River basins about 100 km east of Vancouver at elevations ranging from 120 to 1,360 m (394 to 4,462 ft). They contrasted sites as recently clearcut (<10 years old), second-growth (>25 years old), or old-growth (never harvested: 250+ years old).

[289] In particular, Richardson and Neill (1998) recorded *A. truei* larvae at 54% of 39 clearcut sites, 46% of 69 second-growth sites, and 54% of 36 old-growth sites. Effort used to obtain these occupancy data were not specified, but presumed to be equivalent among sites for the comparison to be valid.

sites.[290] They suggested that the latter observations could be explained by at least two hypotheses: 1) clearcuts impair survival resulting in age- or size-frequency distributions skewed towards smaller larvae (having less mass); and 2) clearcuts enhance development (perhaps from higher temperatures and greater primary productivity) such that animals metamorphose earlier and at a smaller size. Their second-growth site results were equally interesting. Both density and biomass (per unit area) were less than a third of the same measures for populations in old-growth or clearcut sites.[291] Richardson and Neill (1998) suggested three interpretations for this pattern: 1) intense shading in second-growth reduces primary production (larval food); 2) fine sediment intrusion into the streambed, which is slow to develop but has become significant in reducing larval refugia; or 3) a combination of both processes. Considering data collectively, Richardson and Neill (1998) then offered five hypotheses that might explain the occurrence of species that have been characterized as old growth-dependent, such as *A. truei*, in streams flowing through early seral forests: 1) those habitats are sinks for larvae emigrating from upstream or downstream late seral refuge habitats; 2) these are population remnants slowly headed for extirpation; 3) habitat with low larval survival and recruitment is rarely recolonized by adults laying eggs; 4) disturbed sites have fewer places for larvae to hide, making them more susceptible to predation than in undisturbed sites; and 5) forest harvest has no impact. Notably, their fourth hypothesis suggested that detectability was an emerging consideration. The Richardson and Neill (1998) review offered alternative testable hypotheses in addition to the hypotheses provided by Bury and Corn's (1988b) post-harvest conceptual model.

Most studies examining forestry practices and stream-associated amphibians address harvest effects, but forestry practices include activities other than harvest.[292] One such activity is building roads to access harvest sites. Road building is well known to increase sediment streams receive (Beschta 1978, Sauder *et al*. 1987, Rollerson *et al*. 1997, Jakob 1999, Millard 1999). Erosion of unpaved surfaces can produce substantial sediment; at high levels of traffic, unpaved roads can produce up to 130 times more sediment than abandoned roads (Reid and Dunne 1984). Yet, sedimentation effects on amphibians, and specifically *A. truei*, that results from road building, was unaddressed until Welsh and Ollivier's (1998) study. That study contrasted five streams whose headwaters were intersected by the Redwood National Park Highway 101 bypass construction[293] with five streams not affected by construction. Welsh and Ollivier (1998) sampled these streams in June-August 1990, 8-10 months after having received >12.7 cm (5.0 in) of precipitation during an October 1989 storm that mobilized much sediment from highway construction. To sample amphibians, Welsh and Ollivier (1998) used cross-stream belt transects. Selection of belt locations used a stratified sampling design based on stream length and

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[290] Though Richardson and Neill (1998) found no significant differences in larval densities between clearcut and old-growth sites, densities averaged slightly higher on clearcut sites. Richardson and Neill (1998) also indicated that they counted and weighed larvae in defined reaches using standard methods (based on Bury and Corn 1991). However, larvae were not grouped by age class, so the meaning of differences in larval mass is unclear.

[291] Differences in density were significant at $\alpha < 0.05$, but the differences in biomass were not. Evaluation of the degree of difference for the latter is not possible because they reported α as greater than 0.05.

[292] Site preparation [slash removal by various methods, fertilizer application], planting, road building, and thinning are a non-exhaustive list of activities under the heading of forestry practices.

[293] The Redwood National Park Highway 101 bypass actually intersected the headwaters of seven streams, but only five of these were selected for this study (Welsh and Ollivier 1998).

the ratios of primary mesohabitat types along each stream.[294] To evaluate sediment loads, Welsh and Ollivier (1998) measured fine sediment depth and estimated embeddedness of coarse substrates in pool mesohabitats.[295] They found that impacted streams had greater pool tail embeddedness and greater pool sediment depth than unimpacted streams.[296] Using a partial hierarchical ANOVA, Welsh and Ollivier (1998) found an interaction between a sedimentation effect and mesohabitat type on *A. truei* density. In impacted streams, larval tailed frog density was greater in riffles than other mesohabitats, whereas in unimpacted streams, densities were greater in both step runs and riffles when compared to other mesohabitats. Welsh and Ollivier (1998) interpreted this pattern to reflect specialization for riffles in impacted streams because sedimentation affected other mesohabitats in those streams to a greater degree. Using analysis of covariance, Welsh and Olliver (1998) also found that the covariate model for percent embeddedness was significant for *A. truei*, that is, for the covariates examined,[297] most variability reflected percent embeddedness. Importantly, Welsh and Olliver (1998) found no significant differences with respect to the impact of sedimentation on *A. truei* in models adjusted for percent embeddedness, indicating that no further differences could be explained (based on other measured covariates) once the data were adjusted for percent embeddedness. The results of Welsh and Ollivier (1998) suggest a sedimentation impact, but two aspects of their selection of streams (impacted versus unimpacted) create interpretational ambiguities. These include: 1) bias in drainage area, stream order, and stream network patterns such that most impacted streams had larger drainage areas, high-order reaches, and more tributaries than unimpacted streams; and 2) non-independence of samples resulting from the selection of more one "stream unit" in the same drainage.[298] The most

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[294] Welsh and Oliver (1998) based their approach on Welsh and colleagues (1997). Working upstream from Highway 101, they sampled the first unit of every mesohabitat type they found, then randomly selected a unit of each type between the second and the sixth, then every fifth unit of each type thereafter. This provided sampling effort for each mesohabitat type proportional to its availability in each stream. Within each selected mesohabitat type, they systematically placed one or more cross-stream belt transects (belts) based on habitat length, placing one belt for every 10 m of habitat. Belts were 0.6 m wide and extended from bank to bank so that sampling unit length varied with stream width. Length of each mesohabitat unit was divided by the total number of belts desired (about one every 10 m) to determine exact spacing, and a randomly chosen distance between 0 and 10 m was used to place the first belt. Each belt was thoroughly searched for amphibians by first scanning for visible animals and then removing all moveable cover objects. Welsh and Oliver (1998) were confident that their searches captured all amphibians in the open, and likely most under the first layer of unconsolidated substrate where substrate clasts were >16 mm dia.

[295] Welsh and Oliver (1998) measured fine sediment depth at three locations in each pool bowl (the upstream and downstream ends and the middle), which were averaged for analysis. They visually estimated the percentage of embedded coarse substrate at the pool tail.

[296] In impacted streams, tail pool embeddedness averaged 62.6% (standard error of the mean (SE) = 3.9%) and sediment depth averaged 1.52 cm (SE = 0.36), but in unimpacted streams, tail pool embeddedness averaged 44.2% (SE = 3.2%) and sediment depth averaged 0.31 cm (SE = 0.08).

[297] All covariates that Welsh and Ollivier (1998) examined were intended to reflect some linkage with sedimentation. Besides percent embeddedness, percent fines and volume of sand were the other covariates examined.

[298] Four of the five impacted streams (Ten Tapo, Brown, Big Tree, and Boyes Creeks) have drainages 2-5 times larger than four of the five unimpacted streams (Sweet, Good, Corkscrew, and the South Fork of Big Tree Creek).The number of tributaries of the five impacted creeks averaged 19 (range: 4-34), whereas the number of tributaries of the five unimpacted creeks averaged 11 (range: 3-35). Non-independence of streams occurred in the selection of three streams (Big Tree Creek, and its North and South Forks) in that the South Fork of Big Tree Creek (an unimpacted stream) is a second-order tributary of Big Tree Creek (an impacted stream), and the North Fork of Big Tree Creek (also an unimpacted stream) is also a 2nd-order tributary of Big Tree Creek. Welsh and Ollivier (1998) specified that sampling occurred from Highway 101 upstream, so data obtained from the lower reaches of Big Tree Creek would have been influenced by both impacted and unimpacted reaches of this drainage. Even if we allow that sampling occurred only in reaches affected by those tributaries, the Big Tree Creek mainstem up to the North Fork it is not independent of the North Fork of Big Tree Creek.

substantial problem this creates is that the likelihood of *A. truei* occupancy increases significantly with stream order (and stream size), likely as function of wetted channel length (see Hayes *et al*. 2006). If that pattern translates to *A. truei* abundance, Welsh and Ollivier (1998) abundance data was biased for a sedimentation effect. With the lack of independence in stream selection, these conditions complicate interpretation of the results of this study. Nonetheless, this study does contribute to the broadening literature demonstrating that sedimentation from road construction is significant, and provides a basis for future studies to examine the effects on *A. truei* for conditions typical for logging roads. Lastly, when translating the results of this study, two effects of scale are important to consider: 1) Welsh and Ollivier (1998) examined disturbance resulting from a strip for a four-lane divided highway, whereas logging roads are, at most, two narrow lanes; and 2) evaluation of sedimentation occurred following a catastrophic storm event, rather than storms more typical of PNW winter conditions.

In a retrospective study on timber-managed lands in northwestern California, Diller and Wallace (1999) examined 72 near-coastal headwater streams[299] to refine understanding of how *A. truei* occurrence varied across the managed landscape. They found *A. truei* larvae in 54 (75%) of these streams. Using regression analysis, they found lithology to be the better of only two significant predictors (the other was forest age) among five variables[300] examined for a model predicting *A. truei* presence. Eighty-one percent (54 of 67) of streams flowing through consolidated lithologies[301] had *A. truei*, whereas none of five streams they sampled on unconsolidated lithologies contained *A. truei*. The correct classification rate of 86% was undoubtedly underestimated since fieldwork showed that several streams lacking *A. truei* that were classified from maps as being on consolidated lithologies actually had a high proportion of material from unconsolidated lithologies. Forest age was also demonstrated to be a significant predictor of occupancy, but in contrast to previous studies (Bury and Corn 1989, Welsh 1990), Diller and Wallace (1999) showed that occupancy decreased with forest age. Diller and Wallace (1998) believed that this relationship reflected past timber harvest patterns, rather than *A. truei* favoring young forest-dominated landscapes. They indicated that coastal forests, where unconsolidated lithologies were more likely, had been harvested first (late 1800s to early 1900s) and now constitute the oldest second-growth forests. In contrast, more interior sites with steeper, less accessible topography on consolidated lithologies had been harvested within the last 30 years. As a consequence, Diller and Wallace (1998) believed that lithology has such a profound influence on stream substrate condition that it negated the potential impact of stand age on the occurrence of tailed frogs in their region. Using a stream-reach level survey, Diller and Wallace (1998) also found no significant differences in temperature between streams in which *A. truei* was found versus was not

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[299] The study area was located west of the crest of the Coast Ranges mostly within 32 km (20 mi) of the coast, but extending inland up to 85 km in places (Diller and Wallace 1998). All streams in this study were first- or second-order.

[300] The other three variables examined were aspect, elevation, and cover type.

[301] Diller and Wallace (1999) obtained data on lithology from USGS topographic maps, State of California Department of Forestry geology maps, and consultation with a geologist. Thirteen formations identified were grouped into two categories, consolidated and unconsolidated, based on formation age and particle type formed during decomposition. The consolidated group was composed of older formations that form boulders, cobbles, and gravel during decomposition into fine sediments, whereas the unconsolidated group were younger marine deposits that decompose directly into silt and sand.

found,[302] and explained the difference as a function of the attenuating influence of the cool coastal climate for their study region. That explanation may be correct, but their temperature data was collected only during single visits and their sample size of *A. truei*-occupied sites was relatively low. The value of the Diller and Wallace (1998) study lies in having identified lithology as at least a regional-level control on *A. truei* occurrence and having identified the moderating influence of the near-coastal climate on *A. truei* habitat in managed landscapes.

In a retrospective study in northwestern British Columbia, Dupuis and Steventon (1999) examined 54 streams[303] having one of three treatments: 1) old-growth (unharvested); 2) clear-cut without buffers; and 3) clear-cut with buffers.[304] They estimated larval tailed frog density in each stream from searches of three 5-m reaches.[305] Density of larval *A. truei* differed significantly among treatments; the mean density in buffered clearcuts was 1.3 times that in old-growth and 5.7 times that in unbuffered clearcuts ($F_{df(2,51)} = 3.74$, $P = 0.061$).[306] Larval *A. truei* density was inversely correlated with levels of fine sediments ($r = -0.80$), wood ($r = -0.80$), and detritus ($r = -0.72$), and positively correlated with stream width ($r = 0.69$) and levels of rubble ($r = 0.62$). Factor analysis revealed that variables dealing with structure of the stream (bankfull width and levels of fine sediment, wood, and detritus, i.e., Principal Component 1 [PC1]) explained 28% of the variance in *A. truei* density (28%), and climate-linked variables (elevation and water temperature [PC2]) and topographic variables (aspect and gradient [PC3]) explained 21% and 18% of variance, respectively.[307] Larval *A. truei* density was significantly correlated with PC1 and PC3. Larval *A. truei* densities were more than four times higher in streams with

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[302] In their stream-reach surveys, Diller and Wallace (1990) found *A. truei* in 18 of 49 streams. Streams with *A. truei* had median water temperatures of 12.0°C and mean water temperatures of 12.2°C ± 1.7°C SD, whereas streams where *A. truei* was not recorded had median water temperatures of 12.5°C and mean water temperatures of 12.8°C ± 1.3°C SD. Medians temperature compared with a Mann Whitney U test (the data were not normally distributed) were not significantly different.

[303] Dupuis and Steventon (1999) use the terms creeks and streams to have highly specific meanings in a geomorphological context. We used the terms synonymously throughout this paper without regard to geomorphological specifics and discuss all flowing water units treated by Dupuis and Steventon (1999) as simply streams.

[304] Both clear-cut treatments involved forests in the 0-15 year old range. Buffer widths on buffered clear-cut treatments ranged from 5 to 60 m. Dupuis and Steventon (1999) selected three permanent creeks for each treatment within six drainages (Shannon Creek, Carpenter Creek, Kleanza Creek, Copper River, Trapline Creek, and Clore River), a regional stratification that helped control for potential differences among drainages. Streams ranged from 0.5 to 6.4 m in wetted width (1.0-15.0 m in bankfull width) and 200-660 m (656-2,165 ft) in elevation. How selection of streams within each drainage was done was not specified, but Dupuis and Steventon (1999) indicated that most road-accessible creeks within each drainage were surveyed. Thus, they indicated that their sampling density was high and likely representative of larval populations and distributions within each drainage. However, what proportion of the landscape constituted road-accessible creeks is also unclear.

[305] Dupuis and Steventon (1999) located the first 5-m reach randomly and the subsequent two reaches were each spaced by 50 m. Density was estimated for each 5-m reach from the total number of larvae found during a single pass divided by the search area (5 m × the wetted width).

[306] Dupuis and Steventon (1999) used a randomized block ANOVA design to examine differences in mean densities of *A. truei* larvae among treatments with drainage as the blocking factor. One stream, described as ephemeral, was removed from the comparison among treatments. They used a rejection criterion (α) of 0.10 for this and subsequent analysis. Sample size in the dataset varied with the analysis because some streams had missing values for selected variables.

[307] Dupuis and Steventon (1999) initially used univariate correlations to examine relationships between creek variables. They then conducted a principal component analysis to examine which of the variables had the greatest contribution to the variance. A multiple regression was done on components with an eigenvalue greater than one to examine their effect on tadpole numbers. The variable "rubble" was an inorganic substrate descriptor in addition to substrate sizes that described angular material as opposed to rounded material based on Howes and Kenk (1988).

<40% fine sediment than in streams with high levels of sand and pebbles.[308] Larvae were absent in wood-filled streams, whereas densities averaged 26.5 ± 12.2 SE in streams with <50% wood. Though Dupuis and Steventon (1999) found significant differences in larval densities among treatments, within treatment variability was high and its basis is not clear. Old-growth sites in two of their six blocks (six sites total) had very low *A. truei* densities (no *A. truei* were recorded on all three streams in one of these two blocks). Lithology was not considered in site selection and Dupuis and Steventon (1999) reference Holland (1976) in stating that the Hazelton Mountains are, "a complex assemblage of igneous, volcanic and sedimentary rocks," so some variability may simply reflect a lithological influence on *A. truei* densities (see Diller and Wallace 1998). It would have been interesting to know how addressing lithology in the study design might have affected their results. The value of the Dupuis and Steventon (1999) study is in its reinforcing the notion of controls on *A. truei* at the level of stream structure, previously noted by Welsh (1990) and Diller and Wallace (1998); and their identification of a harvest effect at the northern end of *A. truei* geographic range.

In southwestern British Columbia in 1997, Kim (1999; later published as Mallory and Richardson 2005) conducted an enclosure-based experiment in two headwater streams in approximately 30-year-old second-growth forest. They manipulated light, nutrient levels, density of *A. truei* larvae, and enclosure size to examine their effects on periphyton standing crop.[309] Light had a strong, positive effect on algae and periphyton production (30-40% greater biomass in unshaded treatments over shaded ones), which translated into a 14% higher larval *A. truei* growth rate in unshaded versus shaded treatment. In contrast, Mallory and Richardson (2005) found little or no effect of nutrient addition, either alone or interacting with any other single factors. Increasing larval density resulted in significant reductions of algal and periphyton standing crop and reductions in larval growth rate. Mallory and Richardson (2005) also pointed out that even though algal and periphyton production were under simultaneous top-down (tadpole grazing) and bottom-up control (light), the relative importance of those effects varied between the two streams they examined despite their structural similarities. In particular, grazing was the primary influence on algal and periphyton production at Klondike Creek, whereas light levels were the primary influence at Dipper Creek. The Mallory and Richardson (2005) study made two important contributions to the ecology of *A. truei* in managed landscapes: 1) it unambiguously confirmed that streams in the high latitude range of *A. truei* could be light-limited, which via periphyton production, translates to growth effects on grazing larvae; and 2) it showed yet another way that tailed frog responses could be stream-specific within a region.

On the Malcolm Knapp Research Forest in southwestern British Columbia, Maxcy (2000) conducted an experiment from 1997 to 1999 at six sites where three treatments

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[308] Pebbles refers to grain size diameters equivalent to gravels (2-64 mm).

[309] Mallory and Richardson (2005) used periphyton to encompass algae and total periphytic biomass. They manipulated light (shaded vs. unshaded) using 90% industrial shade cloth to simulate closed canopy, and nutrient levels (ambient vs. elevated) using slow-release pellets deposited 10 m upstream of half the enclosures because nutrients cannot be applied randomly to enclosures to achieve experimentally controllable nutrient levels. Enclosure size was controlled, where medium [0.070 m^2] and large [0.105 m^2] enclosures were two and three times, respectively, the size of small enclosures [0.035 m^2]). Density of *A. truei* was manipulated as six levels (0, 10, 14, 29, 57, and 86 larvae/m^2) by adding zero, one, two or three larvae to the small enclosures to produce densities of 0, 29, 57 or 86 larvae/m^2; and adding one larva each to the medium and large enclosures to produce densities, respectively, of 10 and 14 larvae/m^2.

were each replicated twice. Treatments included : 1) unharvested controls; 2) harvest units that retained a 30-m stream buffer; and 3) clear-cuts. This study used pitfall trap arrays, single pitfall traps and cover boards to determine the movement direction of amphibians in a pre- versus post-harvest contrast.[310] Though *A. truei* was found at all sites, high inter-site variation existed in capture rates.[311] Maxcy (2000) had enough captures for analysis at two sites: a control and a 30-m buffer, and analyzed the data as a case study. Based on capture effort calculation, relative abundance declined 50% and 28% between pre- and post-harvest, respectively, in the control and 30-m buffer site.[312] Even ignoring the problems with this kind of relative abundance information, the decline being in the same direction implies a year effect. Maxcy (2000) also provided spatial data for *A. truei* from these two sites. In particular, 57% of captures pre-harvest were within 30 m of the stream at the control site, whereas 40% were within 30 m of the stream in the 30-m buffer site. The post-harvest pattern was reversed; 37% of captures occurred within 30 m from the stream in the control site, and 83% of captures were similarly located in the 30-m buffer treatment. It is tempting to interpret that most captures post-harvest that occurred in 30-m buffer treatment reflected a response. However, lack of partitioning of captures into juvenile and adult stages, which display different behaviors, prevents determining what proportion of captures belonged to each life stage during the pre- versus post-harvest intervals. Maxcy (2000) also provided information on directional movement patterns, which were deduced from her quadri-directional trap arrays (see footnote 310). Post-harvest, the percentage of frogs interpreted as moving parallel to the stream increased by about 25% in the control site and by almost 20% in the 30-m buffer treatment. Similar to her capture effort-based relative abundance data and ignoring movement interpretation issues from quadri-directional traps, the similarity of the change does not support a treatment effect. The value of the Maxcy (2000) study was in its novel method of sampling that may have promise if it can be shown to demonstrate movement direction.

In a retrospective study involving the managed forest landscape in western Washington done 1992 to 1994, Aubry (2000) sampled amphibians with pitfall traps on 24 sites as six replicates of four forest age classes (ages [as years] in parentheses):[313] 1) clear-cut (2-3); 2) pre-canopy (12-20); 3) closed canopy (30-40); and 4) rotation age (50-70). *Ascaphus truei* was captured in all four forest age classes, but in numbers too few for analysis.[314]

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[310] Maxcy (2000) set up pitfall trap grids, single pitfall traps and cover boards in a 50 m × 50 m grid at each site. Pitfall grids consisted of three parallel lines of three pitfall arrays at 5, 30, and 55 m distances from the stream. In each array, four pitfall traps were buried flush with the ground and installed such that one trap each was oriented in the four "cardinal" directions relative to the stream: downslope, upslope, downstream and upstream. This arrangement was designed to assess movement direction relative to the stream for captured amphibians. Sixteen cover boards and six single pitfall traps were also installed at regular intervals in the spaces between pitfall arrays to increase capture probabilities.

[311] Pre- and post-harvest coefficients of variation, respectively, were 107% and 120% (Maxcy 2000).

[312] Trap captured effort was based on the number of individuals caught per 100 trap nights (Maxcy 2000).

[313] Aubry (2000) selected 24 sites in intensively managed landscapes that were completely harvested in the last 70-80 years to minimize any potential influence of residual old-growth on amphibian populations in these second-growth stands. All sites were on the west slope of the central Washington Cascade Mountains; 20 sites were on the Kapowsin and Buckley Tree Farms and the remaining four sites were on the Vail Tree Farm, owned and managed Champion Pacific Timberlands and Weyerhaeuser. Aubry (2000) installed 36 traps in each stand in a 6 × 6 array with 15-m spacing between traps and a >50-m buffer to the edge of the stand. Traps were opened for 28-30 days after the onset of fall rains for three consecutive years (1992 - 94) and checked once per week.

[314] Numbers of *A. truei* trapped in parens for each age class: clear-cut (1), pre-canopy (9), closed canopy (1), and

The value of the study of Aubry (2000) was for the amphibian assemblage excluding *A. truei*.

In another retrospective study focused on the managed landscape in coastal Washington was done in 1995 and 1996. In that study, Wilkins and Peterson (2000) sampled the entire amphibian assemblage in 40 perennial headwater streams within second-growth forests that were near rotation age (50-65 years old). Sampling sites were randomly stratified among the two major lithologies (marine sediment and basalt) and eight major stream basins in approximate proportion to their perennial non-fish-bearing channel lengths.[315] Only 22 *A. truei* were detected in this study in only five streams,[316] all of which were on basalt lithologies. This study had few data on *A. truei*, but it supported the suggestion of Diller and Wallace (1998) of a lithology control on *A. truei* occurrence.

In a retrospective study done in southwestern British Columbia, Matsuda (2001; later published as Matsuda and Richardson 2005) contrasted three clear-cuts with three mature forest sites to assess potential differences in post-metamorphic *A. truei* abundance and movement patterns. Sampling was done with pitfall trap grids with drift fence arrays.[317] Total frog abundance was similar between the two managed forest types.[318] On average, Matsuda and Richardson (2005) captured more than twice the adults in mature than in clear-cuts stands, but found no significant difference in abundance for juveniles.[319] Neither direction of movement or distance from the stream differed between forest types for any age-class. Notably, both the ANOVA and ANCOVA analyses that Matsuda and Richardson (2005) performed indicated substantial site effects (a term in both), and were significant for all post-metamorphic stages combined and juveniles (their immatures). In particular, site effects were greater than the effects of forest type (habitat term in the analyses) for either age class grouping. Matsuda and Richardson (2005) concluded that age-specific differences exist in tailed frog abundance in clear-cuts along streams relative

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rotation age (4).

[315] Wilkins and Peterson (2000) sampled 20 streams each year (9 basalt and 11 marine sediment) during the low-flow period (20 June to 31 August). They established a 100-m channel segment upstream from an arbitrary point of entry to each stream. In each segment, Wilkins and Peterson (2000) collected amphibians from three 5-m channel units. Each channel unit was established at the downstream boundary of each third of the 100 m sampling segment. Prior to searching for amphibians, they blocked off the ends of each channel unit with aluminum screening. During the search, they removed all cover objects >5 cm in diameter and hand-sifted finer substrates. They searched the immediate streambank for amphibians by removing vegetation and organic debris to bare mineral soil in a 1 m band immediately parallel to both sides of the wetted margin of each channel unit.

[316] In their Table 1, Wilkins and Peterson (2000) reported three streams, but in the text, the number of *A. truei*-occupied streams was given as five. The text has the correct number (N. Wilkins, pers. comm.).

[317] Matsuda and Richardson (2005) established 16 drift-fence arrays at each study site. They spaced arrays 20 m apart in a 4 × 4 grid. Each array was a cluster of four pitfall traps similar to the quadri-directional trap arrays of Maxcy (2000) except that they were quartered by four guiding “drift” fences to improve confidence in the directional orientation of amphibians that became trapped. Grids were located near streams at each site such that arrays closest to the streams were within 5 m of the stream margin. Closest distance of the adjacent upstream arrays was 25 m, 45 m, and 65 m.

[318] Eighty-eight *A. truei* were captured in mature stands, whereas 87 *A. truei* were recorded in clear-cuts (Matsuda and Richardson 2005).

[319] Matsuda and Richardson (2005) obtained this result in two separate analyses, an ANOVA designed to examine movement direction and habitat type using the number of frog captures in each age class; and an ANCOVA designed to examine the effects of habitat type and distance from the stream using the number of frogs captured for each age class. In both cases, the natural logarithm of the number of frog captures plus 1 was used to do the analysis. For adults, the probability of a difference between clear-cut and mature forest habitats was 0.05 in the ANOVA; in the ANCOVA, the same was 0.04. The only other age class difference that Matsuda and Richardson (2005) identified was for subadults, and that difference only appeared in the ANOVA ($P = 0.04$), not in the ANCOVA.

to mature forests. They opined that few adults in clearcuts meant that juveniles may be transient or that they incurred high rates of mortality, but their data cannot effectively distinguish this hypothesis from alternatives, including one indicating that juveniles may favor selected habitat conditions existing in clear-cuts. The value of the study of Matsuda and Richardson (2005) is in reinforcing the notion that site effects are important, in their case, more important than the treatment, at least for some life stages. Given the large inter-site variation they found, their conclusion that adult *A. truei* numbers are low in clear-cuts also deserves attention.

In another experimental study in southwestern British Columbia, Kiffney and Richardson (2001) manipulated stream nutrient supply and *A. truei* tadpole density in an artificial channel experiment intended to mimic the environment of fishless headwater streams.[320] Units with and without each of nutrients and larvae were each replicated three times. Because low light levels can limit primary production, Kiffney and Richardson (2001) left channels mostly unshaded.[321] Nutrients were enhanced with slow-release pellets.[322] Larval *A. truei* were added to six channels, three of which had received nutrients, at a rate of 10/channel (equivalent to a density of 3.3/m^2).[323] In channels with added nutrients, periphyton and insect grazer abundance was significantly higher than in the unenriched controls. Growth rates of *A. truei* larvae in nutrient-enriched channels were about four times that of unenriched controls. Insect grazer abundance in all channels was lower in the presence of larval *A. truei*, but the reduction was greater in channels with nutrients. This result is interesting given that Kiffney and Richardson (2001) found no effect of *A. truei* larvae on periphyton biomass. The value of the study of Kiffney and Richardson (2001) lies in demonstrating that *A. truei* larvae in headwater streams can be nutrient limited if light is not limiting, as might be expected in recently harvested headwater streams. As Kiffney and Richardson (2001) indicate, this suggests that at the latitude of British Columbia, *A. truei* may be resource-limited in many headwaters; this also implies that *A. truei* may develop at a faster rate and/or undergo metamorphosis earlier in productive versus unproductive streams.

In a three-year landscape study (1996-1998), Adams and Bury (2000, 2002) examined the relationships of stream-associated amphibians, including *A. truei*, over a large unmanaged landscape, Olympic National Park. An important focus was to improve understanding of stream-associated amphibian ecology through comparison to studies on both managed and unmanaged landscapes. Adams and Bury (2002) surveyed 163 headwater streams (see p. 26 for additional details), which represent 12 of the 13 major

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[320] Kiffney and Richardson (2001) used twelve 15 m × 0.2 m artificial stream channels on a floodplain next to Mayfly Creek from 11 August to 17 September 1997. Water was redirected from the creek 100 m upstream of the channels and passed through two settling boxes and a headbox to stabilize flows. Mean channel slope was 3%, and flow was about 0.5 L/sec and did not differ among channels. Immigration of *A. truei* larvae into channels was limited by a net (250 µm) placed over outflow pipes from the headbox that captured all incoming larvae.

[321] The experiments of Kim (1999), which clearly show light limitation on *A. truei*, were conducted August-September 1997, concurrent with this study, so unambiguous data on light limitation were not yet available.

[322] Slow-release fertilizing pellets were used to increase the phosphorus concentration, which Kiffney and Richardson (2001) hypothesized limited periphyton because channels received full sunlight. In pellets, phosphorus exists as phosphate, whereas nitrogen is ammonia nitrogen. To reach a concentration of 5 µg/L dissolved phosphate based on channel flow rates, they added 88.5 mg of pellets to six randomly assigned channels, three of which received *A. truei* larvae. Phosphorus levels in enriched channels were 1.7 times higher than the levels in non-enriched controls.

[323] This density is intermediate relative to the range of larval densities that has been recorded in the field.

drainages in Olympia National Park.[324] During stream surveys, they sampled amphibians and gathered data on environmental variables.[325] In general, Adams and Bury (2002) found all three stream-associated amphibians, including *A. truei*, most abundant on the southwest Olympic Peninsula, a pattern that they attributed to the southwest-northeast gradient in precipitation across the Peninsula. They also reported that all stream amphibians, including *A. truei*, as common (both in occurrence and abundance) on unconsolidated surface lithologies, such as erodable marine sediments. They used this finding to support that idea that stronger association exists between stream amphibians and surface lithology on managed versus unmanaged landscapes. That is, unconsolidated lithologies increase the sensitivity of stream amphibians to timber harvest. Moreover, they indicated that considering streams with unconsolidated lithologies as a low priority for stream amphibians, as Wilkins and Peterson (2000) suggested, is premature, and implementing any recommendations for conservation based solely on studies in managed landscapes is problematic. No question that caution should be a given when implementing conservation recommendations based on a subset of the landscape. The sensitivity to unconsolidated lithologies hypothesis, as Adams and Bury (2002) proposed, deserves consideration, but alternative hypotheses also need consideration because lithologies at the scale of the Olympic Peninsula were more diverse than those sampled by Wilkins and Peterson (2000). The contribution of Adams and Bury (2002) was pointing out a potential lithology-based difference in amphibian occupancy that may reflect differences between managed and unmanaged landscapes.

Examining the relationships of stream-associated amphibians at three spatial scales, Stoddard (2002; published as Stoddard and Hayes 2005) showed that the presence of a riparian forest stand and its width were variables that most strongly predicted *A. truei* adult or larval occupancy at one or more of the spatial scales (see DISTRIBUTION SUMMARY section, p. 20). Also as noted earlier (see DISTRIBUTION SUMMARY section, p. 22), the importance of the Stoddard and Hayes (2005) study was that it provided evidence that a riparian management zone (as in the presence of a buffer) and the width of that stand could influence *A. truei* occupancy in central coastal Oregon.

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[324] Adams and Bury (2001) sampled each stream once during June-August. Trails and roads were used as a network of non-random transects because of the difficulties of accessing much of the Park. The population of streams from which study sites were chosen was determined by hiking roads and trails in late summer or fall and recording the location of streams with flowing water. In each drainage, one-third to one-half of the streams crossed by main trails and roads were randomly selected. The proportion varied due to drainage-specific constraints. Streams selected were only those that appeared permanent. Large streams (average depths >30 cm) were excluded because the survey approach was ineffective in large streams and the target species were thought to occur predominantly in headwaters. Streams surveyed, generally ≥50 m apart, were considered independent. Sampling only occurred in areas adjacent to trails and roads and thus inferences from the study are theoretically limited to stream reaches directly above trails and roads. Because tadpoles and metamorphic frogs are present during the entire season (summer) in which they sampled, Adams and Bury (2001) did not correct for seasonal changes in abundance. Crews of two or four visited randomly chosen streams, established starting points 30 m upstream of the entry trail or road, and randomly chose 10 stream width-spanning 1-m long stream segments out of the next 100 meters.

[325] Adams and Bury (2001) sampled amphibians in each 1-m segment by overturning rocks and debris directly upstream from a dip net held flush to the substrate. Amphibians disturbed during this search were captured, processed, and released at the point of capture. They also recorded 11 environmental variables at each stream sampled. Three characteristics (gradient, aspect, and elevation) were recorded for the 100-m sample reach. The remaining variables (stream width, depth, dominant and subdominant substrate type, and percent cover of each of coarse woody debris (CWD), other organic debris, undercut bank, and overhanging vegetation) were recorded for 1-m stream segments. Two variables (surface lithology [as geology] and primary vegetation) were obtained from GIS.

To address potential forestry practices effects late in the harvest rotation (as opposed to immediate effects), Ashton and colleagues (2006) compared the relative abundance (and species richness) of stream-associated amphibians in late- versus mid-seral redwood forests of northwestern California.[326] Amphibians were sampled using headlamp-assisted nocturnal visual encounter surveys (VES) over two years (2000-2001).[327] Ashton and colleagues (2006) also measured three factors believed to be important to stream-associated amphibians based on previous research: water temperature, air temperature, and fine sediments.[328] Using count data for post-metamorphic *A. truei*[329] from all three seasons in each year, Ashton and colleagues (2006) found a significantly more post-metamorphic *A. truei* in late-seral than mid-seral sites.[330] They also found significantly more recently metamorphosed individuals in the fall than in the other two seasons.[331] High variability in numbers of recently metamorphosed individuals in reaches within streams and streams within seral stage led Ashton and colleagues (2006) to re-analyze their data excluding this life stage.[332] This analysis revealed that difference in numbers between seral stages remained significant, but in this case, 98.6% of adult and subadult *A. truei* detections were the late-seral streams.[333] Though the data of Ashton and colleagues appear to support an unambiguous conclusion of greater numbers of *A. truei* in late-seral over mid-seral stages, the study suffers from at least one key bias: late-seral basin size was 2.4 to 10 times that of its mid-seral counterpart in three of six basin pairs.[334] A strong

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[326] Ashton and colleagues (2006) selected three pairs of streams in each of two blocks. The two blocks were near large areas of relatively undisturbed late-seral Coast Redwood forest in northern and southern Humboldt County. Both blocks were classified in the same Central Franciscan subsection of the Northern Redwood Forest section based on Sawyer and colleagues (2000), but differences in understory vegetation and substrate composition existed between blocks. One stream in each pair was chosen from a mid-seral grouping (stands 37-60 years since harvest), whereas the other was selected from a late-seral grouping (little evidence of human disturbance with some trees >150 years old). Ashton and colleagues (2006) selected pairs of streams to minimize within-pair differences in aspect, gradient, elevation, and distance to coast. Ashton and colleagues (2006) mapped a 200 m of each stream to serve as the frame from which sampling units were selected. That 200 m reach was divided into 10 20-m long units from which three were randomly selected for amphibian sampling.

[327] Ashton and colleagues (2006) VES-sampled each stream in each of three seasons: spring (28 April–1 June 2000, and 26 April–6 June 2001), summer (2 July–1 August 2000, and 17 July–17 August 2001), and fall (23 September–27 October 2000, and 16 October–1 December 2001). All post-metamorphic amphibians observed within each 20-m unit were counted, identified to species, and sexed,

[328] Ashton and colleagues (2006) measured water and air temperatures with a digital thermometer at the upper end of each sampling reach on each sampling night. Fine sediment loads were measured in each stream using S*, a simplified estimator for V* (Lisle and Hilton 1992), a method to evaluate mobile stream sediments using the ratio of maximum sediment depth to maximum residual pool depth. Ashton and colleagues (2006) randomly selected 10 pools per stream and measured pool sediments at the end of the fall sampling period (see footnote 327) by probing each pool with a calibrated metal rod to measure sediment depth, maximum pool depth, and pool tail depth.

[329] Post-metamorphic *A. truei* included adults, subadults and recently metamorphosed individuals. Larval *A. truei* were excluded from this analysis because the sampling method is not appropriate for quantifying larvae.

[330] $F_{(df)1,8} = 17.61$, $P = 0.0030$; contrasts revealed that late seral numbers (n = 32-154) were greater mid-seral numbers (n = 0-4).

[331] $F_{(df)2,14.1} = 8.60$, $P = 0.0036$; contrasts revealed that fall numbers were greater than each of spring and summer numbers.

[332] Ashton and colleagues (2006) suggested this patchy distribution of recent metamorphs reflected an asynchronous development and transformation from tadpoles, and suggested that too few sample reaches existed to accurately portray the relative quantities of this life stage at the stream level.

[333] $F_{(df)1,31.9} = 63.63$, $P < 0.0001$; contrasts revealed that late seral numbers (n = 14-39) were greater mid-seral numbers (n = 0-1).

[334] The late-seral basin in basin pair N2 (136.5 ha) was 2.4 times the size of the mid-seral basin in this pair (56.3 ha); late-seral basin in basin pair S1 (186.0 ha) was 3.5 times the size of the mid-seral basin in this pair (53.7 ha); and late-seral basin in basin pair S2 (569.6 ha) was 9.9 times the size of the mid-seral basin in this pair (57.5 ha; Ashton *et al.* 2006).

relationship exists between *A. truei* occupancy (or abundance) and basin size (Hunter 1998, Hayes et al. 2006, Kroll et al. 2008), a pattern also demonstrated for *A. montanus* (Dupuis *et al.* 2006). The importance of the study of Ashton and colleagues (2006) is that it is one of the few to address post-metamorphic life stages and it raises the question of potential relative abundance differences for those life stages among seral stages.

In the second of the few studies addressing *A. montanus* landscape ecology, Dupuis and Friele (2006) showed that the species occurs in basins ranging in size from about 0.3 to 100 km^2 (0.1-38.6 mi^2) with peak abundances in basins up to 35 km^2 across its Canadian range. They concluded that this pattern reflects channel processes and stream discharge because *A. montanus* appears adapted to the cascade and step-pool channel morphologies that characterize this range of basin sizes. They speculated that this relationship results from stream channels in this range of basin sizes having: 1) greater bedform stability and pore-space refugia than the smaller channels in colluvial process-dominated headwaters or the fluvial process-dominated larger river channels, and 2) greater transport capacity relative to their limited sediment supply (the latter emphasized by Montgomery and Buffington [1997]). Dupuis and Friele (2006) added that climate and physiography interact on this landscape-level pattern to influence the occurrence and abundance of *A. montanus* through controls on variables such as runoff, water temperature and sedimentation regime. This study has management implications for all tailed frog species because processes within streams exhibit parallel patterns among stream networks (Montgomery and Buffington 1997). For forest practices, this means that protection of cascade and step-pool channel morphologies within basins subject to timber harvest is important for tailed frog conservation. In also means that because runoff, water temperature, sedimentation regime and lithology vary substantially among watersheds, site-specific understanding of fluvial system controls is needed to identify habitat important to tailed frogs in those basins.

In an almost parallel study, Hayes and colleagues (2006) demonstrated the importance of basin size in *A. truei*.[335] This study differed from that of Dupuis and colleagues (2006) in four important ways: 1) it addressed only the non-fish-bearing (headwater) portion of the landscape; 2) it showed that *A. truei* reproduction was not possible in streams with the smallest (first-order) basin sizes because permanent water was either extremely limited or absent; 3) it identified a longitudinal pattern in summer habitat use for all *A. truei* life stages in headwater basins; and 4) it related the basin size requirements for adult *A. truei* to their seasonal movements, which were upstream to the vicinity of the stream origin in late summer. In the state of Washington, forest practice regulations require the placement of a 15.2-m (50-ft) RMZ on both sides of the stream over no less than 50 percent of the headwater stream network. Most of this requirement is met by placing the RMZ[336] along the stream closest to the fish-bearing reaches, which results in less RMZ protection near the stream origin. If step pools and cascades mostly occur near the stream origin, then

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[335] See pages 22, 27, and 43 for additional information about the study of Hayes and colleagues (2006).

[336] Based on Washington Forest Practice Rules, a significant portion of the buffer, the precise length of which varies with headwater stream length, must be placed contiguous to the fish-bearing end of the stream. Additionally, a 15.2-m buffer must be placed around all sensitive sites, which comprise five categories: 1) headwall seeps, 2) side-slope seeps, 3) headwater springs, 4) tributary junctions, and 5) alluvial fans. Though the remaining buffer, up to the minimum 50 percent requirement, can be placed anywhere along the stream that lacks a buffer, forest management entities typically place that buffer immediately upstream of the buffer contiguous with the fish-bearing reach.

Washington regulations may not be protecting the most important adult *A. truei* late summer habitat.

In 1998-2001, Jackson and colleagues (2007) conducted a study using a before-and-after-control-impact (BACI)[337] design to address channel, macroinvertebrate, and amphibian responses to harvest in coastal Washington. They examined 15 first-order[338] streams of which six were clearcut, five were harvested leaving an RMZ,[339] and four historically in the rotation but unharvested for the duration of the study served as references. Though sites were pre-selected for stream-associated amphibian presence,[340] *A. truei* was found in only five of the 15 streams, so for *A. truei*, the results of this study really represent a series of case studies.[341] Of the five *A. truei*-occupied sites, three were complete clearcuts, one was a clearcut with a buffer, and one was a reference. Streams were systematically searched for amphibians using light-touch rubble rousing (Bury and Corn 1991) involving two passes of 10-12 m sample reaches completed on the same day.[342] Post-harvest sampling in streams not buried in slash used the pre-harvest sampling approach, but slash-buried areas were cleared of slash prior to sampling with the same approach.[343] The numbers of *A. truei* dropped from relatively low densities to zero in the three complete clearcuts, and *A. truei* was found in one of these three sites two years post-harvest. The buffered clearcut site counts increased slightly immediately post-harvest and then dropped dramatically two years later, and the reference site counts declined slightly just post-harvest, but increased dramatically two years later. The results of this study are difficult to interpret for *A. truei* because the post-harvest timeline is too short to determine whether recovery of *A. truei* in the clear-cuts was actually occurring. This study likely also suffered because site selection was intentionally broad, encompassing several lithologies. This approach allows generalizing to a larger segment of the landscape, but at the cost of increasing variability. Results of the Wilkins and Peterson (2000) study that revealed a differential in *A. truei* occupancy and abundance between two different lithologies in coastal Washington (see DISTRIBUTIONAL SUMMARY section, p. 19) was not available at the time this study was designed. The value of the study of Jackson and colleagues (2007) was in the case study series that revealed a uniform response across clearcut treatments.

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[337] BACI studies, which involve sampling before and after the application of a treatment, are considered one of the strongest manipulative designs to experimentally determine treatment effects.

[338] Based on the Strahler (1951) stream-order categorization.

[339] RMZs were 8-10 m wide on each side of the stream channel. Three streams had a buffer consisting of merchantable trees along the entire length of the stream, one had a non-merchantable RMZ also over the entire stream length, and the fifth had a RMZ along approximately one-third of the stream length.

[340] Based on a 20-min time-constrained search.

[341] None of the statistical tests found a significant treatment effect for any amphibian species, so Jackson and colleagues (2007) simply discussed the site estimates over the time series.

[342] Jackson and colleagues (2007) placed a net across the stream at the bottom of a survey reach and then searched for amphibians starting upstream and working downstream toward the net. Amphibians were captured by hand or with dip nets, and all cover objects >5 cm in diameter were removed. A second pass of the reach was conducted after the cover objects were removed.

[343] In slash-buried streams, Jackson and colleagues (2007) first cleared an area for the placement of the net at the downstream end of the survey reach. They then removed woody debris from the channel by hand, or by using chainsaws to cut wood into manageable sizes. Large boles and branches of the bucked timber that had come to rest in the channels were removed until they had totally exposed the flowing stream. They then conducted amphibian surveys in a manner identical to the pre-harvest surveys (see footnote 342).

During 1995-1999, Olson and Weaver (2007) studied the vertebrate assemblage at 12 headwater forest sites[344] in western Oregon. At these sites, they characterized amphibian habitat and fauna in 106 headwater reaches over the five-year interval. [345] This study was designed to describe the vertebrate assemblage of these sites prior to thinning selected stands and comparing them to unthinned (reference) stands. Stream habitats were characterized using a modified Hankin and Reeves (1988) approach.[346] Instream vertebrate surveys were conducted following habitat surveys on 10 units (see footnote 345) selected at random per reach. Canonical correlation analysis, non-metric multi-dimensional scaling, and generalized linear models were used to characterize habitats and vertebrate assemblages. Because Olson and Weaver (2007) recorded only 52 *A. truei* over five of the 12 sites, *A. truei* data were only used in canonical correlation analyses. Vertebrate assemblages partitioned by habitat into perennial, intermittent and dry reaches (with both instream and bank components) revealed that *A. truei* was most frequently found in the instream and bank compartments of perennial reaches, infrequently found in intermittent reaches, and never found in dry reaches. All *A. truei* on banks were post-metamorphic life stages, and were much less frequent than life stages found instream in both perennial and intermittent reaches, which were mostly larvae (D. Olson, 2012, *pers. comm.*). Canonical correlation analysis (combining bank and instream compartments) revealed that *A. truei* was one of three taxa[347] with counts strongly positively related (canonical coefficient ≥1.00) to the variables measured.[348] Among examined variables, those showing the strongest positive relationship (canonical coefficient ≥0.25) were stream depth, survey method, and wood density; no variables showed a strong negative

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[344] Sites ranged in size from 47 ha (116 ac) to 279 ha (689 ac); and size was determined from the unit boundaries of the respective treatments (Olson and Weaver 2007). Stands at these sites were 40-80 years old, naturally regenerated from clearcut harvests without stream buffers and consisted of homogeneous forest dominated by Douglas-fir with 430-600 trees per hectare. A distinct riparian zone was generally lacking, that is, forest in the stream edge and upslope were similar in composition.

[345] Olson and Weaver (2007) defined minimum reach length as two site-potential tree heights (110–150 m). Generally, reaches were distinguished by tributary junctions, reach length within the study site boundary, or by the upstream end of water flow. Inclusion of a reach within the survey effort was contingent on a forest thinning treatment being planned in that portion of site; however, inclusion of reaches to characterize the larger basin was also conducted opportunistically. Reaches above stream origins were sampled due to uncertainty of these zero-order basins functioning as streams, or as habitat for stream-associated amphibians. Selected dry reaches had evidence of past scour and deposition. As a consequence, within sites, reaches were not independent because a continuous stream thread from dry to perennial streams may have included more than one reach. Also, for amphibian assemblages, animals may have been able to move overland between neighboring subdrainages even if they were located in different large watersheds such that aquatic connectivity was not an issue.

[346] Reaches were typed during both the wet season (March-June) and dry season (July-September) by walking upstream and measuring or visually estimating habitat parameters (Olson and Weaver 2007). Survey timing tracked local weather such that the sites sampled later in a season were at higher elevations. For each reach, Olson and Weaver (2007) first identified sequential habitat units dominated by no surface flow (dry units) and two types of wet units: slow (pool) or fast water flow (step, cascade, riffle) habitat types. Dry units were variable in length and could have been sections in-filled with side-slope colluvium or downed wood embedded with substrate or other debris. Olson and Weaver (2007) collected several habitat measures in wet units, including unit size (e.g., average depth, length, and width), dominant and subdominant substrate type (as 6 categories, particle diameters in brackets: bedrock [>300 mm]; boulder [101–300 mm]; cobble [30–100 mm]; large gravel [11–30 mm]; small gravel [3–10 mm]; fine substrates [>3 mm], downed wood (tally of large pieces by size, large pieces were ≥1 m long and ≥0.1 m dia), and stream gradient for wetted reaches in four categories: flat (0–5%), moderate (6–15%), moderately steep (16–30%), and steep (>30%). Habitat measures were not collected in dry reaches because the initial focus was to characterize habitats of flowing streams; fauna was sampled in both flowing and dry reaches.

[347] The remaining two taxa were salmonid fishes (*Oncorhynchus* spp.) and Dunn's salamander (*Plethodon dunni*).

[348] Canonical coefficients were 2.30, 1.80, and 1.00 for salmonid fishes, *A. truei* and *Plethodon dunni*, respectively.

relationship.[349] A second canonical correlation analysis addressing only the instream compartment[350] showed that *A. truei* was one of only two taxa with counts moderately positively correlated (canonical coefficient ≥0.75) to the variables measured.[351] Two of the same three variables showed the strongest positive relationship (wood density and survey method) to *A. truei* capture rate, but stream depth now revealed a strong negative relationship to capture rate.[352] The basis of the latter is unclear (D. Olson, G. Weaver, 2012, *pers. comm.*). A third canonical correlation analysis addressing bank-only data was uninterpretable due to small sample sizes (D. Olson, 2012, *pers. comm.*).[353] Olson and Rugger (2007) provided the initial post-treatment results for most of the pre-treatment landscape that Olson and Weaver (2007) described.[354] In their overall summary of captures, Olson and Rugger (2007) presented total bank and instream *A. truei* captures and *A. truei* recorded by sites summarized as pooled observations over one-year pre- and two years post-treatment.[355] This summary revealed that *A. truei* was detected at more sites in both bank (n = 7) and instream (n = 8) surveys than reported for pre-treatment data.[356] However, the report does not describe if more sites were actually occupied in each post-treatment year or whether all five sites described in the pre-treatment study were recorded as occupied in these initial post-treatment years.[357] Relatively constant capture rates between pre- and post-treatment led Olson and Rugger (2007) to conclude that no negative treatment effects from thinning were discernable at any buffer width. Preliminary analyses of 5- and 10-year post-treatment data do not alter this conclusion (D. Olson, 2012, *pers. comm.*). However, the unknown consequences of the complicated study design (seasonal and annual sampling stagger, and complex rotating panel of headwater) and unaddressed treatment- and seasonal-level detectability limits conclusion strength.

In a broad regional study described in the DISTRIBUTION SUMMARY section (p. 23), Kroll and colleagues (2008) sampled 141 perennial non-fish-bearing streams from the managed landscape in western Oregon and Washington. This study evaluated factors influencing occupancy and detection probability for stream-associated amphibians. Kroll and colleagues first modeled covariates that might influence detection probabilities[358] while holding occupancy constant. Second, in an AIC-based model comparison, they then

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[349] Canonical coefficients were 0.96, 0.51, and 0.25 for stream depth, survey method, and wood density, respectively.

[350] This analysis was conducted exclusively with larvae (D. Olson, *personal communication*).

[351] Canonical coefficients were 1.27 and 0.88 for salmonid fishes and *A. truei*, respectively.

[352] Canonical coefficients were 0.47, 0.46, and 0.20 for wood density, stream depth, and survey method, respectively.

[353] Canonical coefficient for bank *A. truei* was 0.10.

[354] Post-treatment results are based in 11 sites (versus 12 pre-treatment) and 68 reaches (versus 106 pre-treatment).

[355] Though analysis was based on one-year of post-treatment data, staggering of sampling across sites led to examining the one-year of post-treatment data that was the temporally most clustered. At least part of the staggering resulted from timber harvest activities occurring in areas next to treatment units so access to some sites was unsafe immediately post-harvest. Year 1 post-harvest data were collected from 0 to 17 months after treatments whereas because of treatment application stagger, Year 2 post-harvest data were collected 11-29 months after treatment application. Hence, for analysis of one year of post-treatment data, the most comparable dates were chosen; this involved five sites within the Year 1 data collection interval that had the later dates of survey within that interval and six sites within the Year 2 data collection interval that had the earlier dates of survey within the latter interval. This most comparable interval analysis encompassed data from 7 to 18 months post-treatment.

[356] This assessment is based on the fact that Olson and Rugger (2007) reported only five of 12 sites examined as being *A. truei*-occupied.

[357] Similarly, numbers of captures by post-treatment year are unavailable.

[358] Covariates examined were sampling (Julian) date, time of day, rain during the survey, rain within a 24-hr period before the survey, cloud cover or sunshine, stand age, and water and air temperature.

examined alternative occupancy models for each stream-associated amphibian taxon that incorporated the best model for detection probability. Kroll and colleagues (2008) found mean detection probability for *A. truei* to be considerably less that 1 ($P_{detection}$ = 0.63). Though no covariate that Kroll and colleagues (2008) measured for *A. truei* detection probability received strong statistical support,[359] *A. truei* detection probability declined 35% between mid-July and mid-October sampling dates.[360] Kroll and colleagues (2008) found empirical support[361] for three models for *A. truei*, which showed that crayfish presence, stand age, and stream size[362] all influenced occupancy. However, they used the model for inference for each of these that incorporated sampling date because of on the seasonal change in detection probability. For bankfull width (reflecting stream size), that model revealed that likelihood of *A. truei* occupancy varied in a quadratic fashion such that the likelihood of occupancy was greatest at intermediate stream sizes[363] and increased in a linear fashion with stand age.[364] They also found that crayfish presence reduced the likelihood of *A. truei* presence regardless of the relationship involved.[365] This study, the first to estimate detection probabilities for stream-associated amphibian species in the PNW, highlights the importance of understanding how likelihood of detecting a species varies with selected covariates. Though no covariates significantly changed detection probability for *A. truei*, this result could reflect the fact that life stages were lumped or that the sampling timeline was short. The study of Kroll and colleagues (2008) is important because it revealed a non-trivial temporal bias in abundance estimates as a function of a declining detection probability through the season. If detection probability varies with a covariate that also changes as a consequence of an experimental treatment, ignoring detection probability has the potential to substantially alter interpretation of study results (MacKenzie *et al*. 2002).

In a second regional study described earlier (p. 23) conducted in 2007-2008, Kroll and colleagues (2010) examined 70 randomly selected third-order basins in the managed landscape of western Oregon and Washington. The study's focus was an effort to address the discrepancy between research and operational scales, and estimate detection and occupancy parameters and develop basin-level density estimates for various stream-associated amphibian taxa and provide a basis for future comparisons to both these same basins and potential contrasts to unmanaged landscapes.[366] They conservatively estimated having detected *A. truei* in 38 of 67 (57%) basins, which included 8 of 10 (80%) basins in the southern Cascades of Washington, 22 of 30 (73%) basins in the Oregon Coast Range, and 8 of 27 (30%) in the Willapa Hills of southwestern Washington. Occupancy patterns for the Willapa Hills were somewhat higher than those reported by Hayes and colleagues (2006) for the Stillman Basin in the Willapa Hills (16% and 19% based on temporally different estimates), but differences may reflect the lack of incorporation of detectability

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[359] The 95% confidence interval for the date included zero.

[360] Mean detection probability for *A. truei* declined from 0.78 in mid-July to 0.42 in mid-October.

[361] A ΔAIC value of $\leq$2.

[362] Used as the square of bankfull width, that is (bankfull width)^2.

[363] Peak likelihood of occupancy was at a bankfull width of roughly 4 m (13 ft).

[364] Over the range of stand ages measured, that is 0 to 70 years.

[365] Depression of the likelihood of occupancy appeared generally uniform (non-interactive) across these relationships.

[366] Though individual harvest units can encompass multiple stream reaches and sometimes entire second-order basins, nearly all published research studies used stream reaches of various lengths as sample units. This effort was an important step to improve the basis for comparisons.

in the latter study, asymmetry in locations (the basins of Kroll and colleagues were uniformly further south) or both. Overall, *A. truei* occupancy probability was estimated to be 0.60 (95% CI = 0.46-0.72). Kroll and colleagues (2010) noted that the occurrence probabilities in third-order basins in managed forests in Oregon and Washington could reflect one of three possibilities: 1) extirpation of *A. truei* from previously occupied basins, assuming 100% occupancy historically; 2) static occupancy over time; and 3) increases in occupancy probabilities under current conditions. They emphasized that without comparable data from unmanaged forests or data collected prior to harvest for the sites they sampled, which of these possibilities was more like could not be determined. Their data represents an important baseline to assess these alternatives in the future and they stressed the importance of management agencies collecting these types of data for public forests not managed for commercial wood or fiber production.

In a study conducted in the Cascade Range in southern Washington, Pollett and colleagues (2010) addressed the effectiveness of stream-side buffers in ameliorating the effects of clearcut harvest on stream-associated amphibians[367] and water temperature regimes. They sampled 41 streams from four categories: streams in clearcuts with and without buffers, streams in 35+ year old second-growth forest, and streams in unharvested forest (150+ years old). Densities of *A. truei* were two to seven-fold lower ($P < 0.05$), respectively, in managed forests streams than in unharvested forest streams. Coastal tailed frogs were also less abundant ($P < 0.05$) in unbuffered streams than streams with buffers or in second-growth forest. Pollett and colleagues (2010) used the differences in density estimates of unbuffered streams and unharvested streams to define an ecologically important effect size. They then compared the mean effect size and 95% confidence intervals between managed stream categories to assess buffer effectiveness (*sensu* DiStefano 2004). Buffers had an ecologically important positive effect on tailed frog density, but interestingly, water temperatures did not differ among stream categories. The importance of this study was in showing the value of stream buffers on factors other than water temperature for tailed frogs at the latitude of southwest Washington.

The most recent published study (Hawkes and Gregory 2012) is a 10-year follow-up to the Kelsey (2000) study, which has the same structure except for a substitution of two new unharvested reference sites because two of the original reference sites had been harvested. Further, instream sampling was excluded from this follow-up because of Kelsey's (1995, 2000) analysis that 100 sites would be need to distinguish treatments effects from this sampling (see earlier discussion). Hawkes and Gregory (2012) recorded a declined in post-metamorphic *A. truei* 10 years post-harvest, but these data incur the same problems of interpreting the abundance of *A. truei* post-metamorphic life stages as do earlier studies using this method.

Summary: Given the number studies that address at least some of this topic (Tables 3 and 4), one might reasonably conclude that the effects of forestry practices on tailed frogs are at least moderately well understood. On the basis of studies to date, however, this review reveals that this assertion remains somewhat remote. We believe this condition arises from the intersection rapid-evolving sampling techniques with at least a historical

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[367] Stream-associated amphibians species addressed were Cascade torrent salamanders (*Rhyacotriton cascadae*), coastal and Cope's giant salamanders [*Dicamptodon tenebrosus* and *D. copei*], and *A. truei*),

underappreciation for variability in local landscapes and perhaps to some extent variation resulting from latitudinal and coastal-to-inland gradients. Further, the peculiar amalgam

Table 3. Characteristics of studies linked to addressing potential effects of forestry practices on tailed frogs in the Pacific Northwest. Ng indicates values not given. In the Strata column, yes indicates one level, where more than one level existed, the number of tiers is show immediately below. In the Reference column, pr indicates a pseudo-reference; one with a critical spatial or temporal confound.

Author(s)	Year		Study Characteristics					
	Publish	Executed	Type	Treatment(s) (# in parens)	Sampling Frame	Strata	Replication	Reference(s) (# in parens)
Aho	1976	1973-1974	Retrospective	(1) Harvested – 8 yr	Mack Creek, OR	No	No	(1) Unharvested (pr)
Murphy and Hall	1981	1976	Retrospective	(10) Clearcut – 5-17 yr (6) 2nd-growth – 12-35 yr	Upper McKenzie River, OR	Yes	Yes	(15) Old-growth – >450 yr
Murphy et al.	1981	1978	Retrospective	(6) Clearcut – 5-10 yr (6) 2nd-growth – 30-40 yr	Upper McKenzie River, OR	Yes	Yes	(6) Old-growth – >450 yr
Hawkins et al	1983	1978-1979	Retrospective	(10) Open 2nd-growth	Central OR Coast & OR Cascades	No	Yes	(10) Shaded 2nd-growth
Bury	1983	1975	Retrospective	(4) Harvested – 6-15 yr	Redwoods National Park & vicinity	No	Yes	(4) Old-growth
Hawkins et al	1988	1985-1987	Retrospective	(6) No forest (3) Headwaters forested	Mt. St. Helens vicinity	Yes	Yes	(4) Forested
Bury and Corn	1988a	1983	Retrospective	(5) Clearcut - <10 yr (6) Young – 30-76 yr (6) Mature – 105-150 yr	SW WA Cascades & Central W OR	Yes	Yes	(15) Old-growth – 195-450 yr
Corn and Bury	1989	1984-1985	Retrospective	(20) Harvest – 14-40 yr	Central OR Coast Range	No	Yes	(23) Unharvested – 60->400 yr
Welsh	1990	1984-1985	Retrospective	(9) Young – 60.0 yr ± 17.7 (9) Mature – 147.1 yr ± 30.4	SW OR & NW CA	Yes	Yes	(21) Old-growth – 344.1 yr ± 17.7
Corn and Bury	1991	1984-1985	Retrospective	(5) Clearcut - <10 yr (8) Young – 40-75 yr (10) Mature – 80-120 yr	Central OR Coast Range	Yes 2-tier	Yes	(27) Old-growth – 150-525 yr

Table 3 (continued). Characteristics of studies linked to addressing potential effects of forestry practices on tailed frogs in the Pacific Northwest. Ng indicates values not given. In the Strata column, yes indicates one level, where more than one level existed, the number of tiers is show immediately below. In the Reference(s) column, pr indicates a pseudo-reference; one with a critical spatial or temporal confound.

Author(s)	Year		Study Characteristics					
	Publish	Executed	Type	Treatment(s) (# in parens)	Sampling Frame	Strata	Replication	Reference(s) (# in parens)
Gilbert and Allwine	1991	1984-1985	Retrospective	(ng) Young – 30-80 yr (ng) Mature – 80-200 yr	Mt. Hood Natl F HJ Andrews EF Upper Rogue-Upper Umpqua	Yes 2-tier	Yes	(ng) Old-growth – >200 yr
Aubry and Hall	1991	1984-1985	Retrospective	(9) Young – 55-75 yr (9) Mature – 80-190 yr	SW WA Cascades	Yes 2-tier	Yes	(9) Old-growth – 210-730 yr
Bury et al.	1991	1984-1985	Retrospective	Additional analyses combining data from Corn and Bury (1991), Gilbert and Allwine (1991) and Aubry and Hall (1991)				
Lamberti et al.	1992	1986	Manipulative	(8) Varying *A. truei* densities (4-96 m^2) in experimental channels	Central W WA Cascades	Yes	Yes	(1) No *A. truei* larvae
Lamberti et al.	1992	1986	Manipulative	(11) Variable *A. truei* density streams; raised periphyton plates	Central W WA Cascades	Yes	Yes	(11) Varying A. *truei* density streams; streambed plates
Lamberti et al.	1992	1986	Manipulative	(1) Hi dens *A. truei* stream (1) Lo dens *A. truei* stream; raised periphyton plates	Central W WA Cascades	Yes	Yes	(1) Hi dens *A. truei* (1) Lo density; streambed plates
Kelsey	1995	1992-1994	Manipulative	(1) Clearcut (6) Clearcut w 20-65 m buf	Central W WA Cascades	Yes	Yes	(3) Unharvested
Bull and Carter	1996a	1993	Retrospective	(10) Low - <20% harvested (10) Moderate – 20-50%	Blue-Wallowa Mountains	Yes	Yes	(10) High - >50% harvested
Richardson and Neill	1995 1998	1994	Retrospective	(39) Clearcut – 0-25 yr post (69) 2nd-growth - >25 yr post	Chilliwack & Skagit areas, BC	Yes	Yes	(36) Old-growth

Table 3 (continued). Characteristics of studies linked to addressing potential effects of forestry practices on tailed frogs in the Pacific Northwest. Ng indicates values not given. In the Strata column, yes indicates one level, where more than one level existed, the number of tiers is show immediately below. In the Reference(s) column, pr indicates a pseudo-reference; one with a critical spatial or temporal confound. An asterisked (*) author column indicates a study not directly involved forestry practices.

Author(s)	Year		Study Characteristics					
	Publish	Executed	Type	Treatment(s) (# in parens)	Sampling Frame	Strata	Replication	Reference(s) (# in parens)
Welsh and Ollivier*	1998	1990	Retrospective	(5) Impacted Streams	Prairie Creek State Redwood & Redwood Natl Park, CA	No	Yes	(5) Non-impacted streams
Diller and Wallace	1999	1993-1996	Retrospective	(72) Headwater streams	NW coastal CA	No	Yes	NA
Dupuis and Steventon	1999	1994	Retrospective	(18) Unbuffered clearcuts (18) Buffered clearcuts Both 0-15 yr; buffers 5-60 m	Skeena River system, BC	Yes 2-tier	Yes	(18) Old-growth – age ns
Kelsey (in O'Connell et al.)	2000	1992-1996	Manipulative	(6) State buffers – $\bar{x}$ =13 m ± 2.0 m SE (6) Modified buffers – $\bar{x}$ = 29 m ± 2.2 SE	SW WA SW WA Cascades	Yes	Yes	(6) Unharvested
Maxcy	2000	1997-1999	Retrospective	(2) Clearcut (2) 30-m buffers	Malcolm Knapp Research Forest BC	Yes	Yes	(2) Unharvested
Aubry	2000	1992-1994	Retrospective	(6) Clearcut – 2-3 yr (6) Pre-canopy – 12-20 yr (6) Closed canopy – 30-40 yr	W Cascades Pierce Co, WA	Yes	Yes	(6) Rotation age – 50-70 yr
Wilkins and Peterson	2000	1996-1997	Retrospective	(22) Marine sediment (18) Basalt	S Gray's Harbor & N Pacific Cos, WA	No	Yes	NA
Wahbe and Bunnell	2001	1995-1999	Retrospective	(3) Recent clearcut - <5 yr (3) 2nd-growth – 60-80 yr	Ashlu, Elaho, Mamquam, & Squamish Basins, BC	Yes	Yes	(3) Old-growth – >250 yr

Table 3 (continued). Characteristics of studies linked to addressing potential effects of forestry practices on tailed frogs in the Pacific Northwest. Ng indicates values not given. In the Strata column, yes indicates one level, where more than one level existed, the number of tiers is show immediately below. In the Reference(s) column, pr indicates a pseudo-reference; one with a critical spatial or temporal confound.

Author(s)	Year		Study Characteristics					
	Publish	Executed	Type	Treatment(s) (# in parens)	Sampling Frame	Strata	Replication	Reference(s) (# in parens)
Kiffney and Richardson	2001	1997	Manipulative	(3) +Nutrients, (3) +ASTR larvae	Mayfly Creek, BC	Yes	Yes	(3) for nutrients, (3) for tadpoles
Adams and Bury	2002	1996-1998	Retrospective	163 Headwater streams – 55-530 cm wide	Olympic National Park, WS	Yes	Yes	NA
Wahbe and Bunnell	2003	1995-1999	Retrospective	(3) Recent clearcut - <5 yr (3) 2nd-growth – 60-80 yr	Elaho, Mamquam, & Squamish Basins, BC	Yes	Yes	(3) Old-growth – >250 yr
Mallory and Richardson	2005	1998	Manipulative	(96) Unshaded (96) Nutrients added (160) 5 larval density levels	Dipper and Klondike Creek in BC Cascades	Yes 3-tier	Yes	(96) Shaded (96) No nutrients (32) No larvae
Matsuda and Richardson	2005	1998-1999	Retrospective	(3) Harvest - <5 yrs post	Chilliwack River Valley, SW BC	No	Yes	(3) 81-yr 2nd growth
Stoddard and Hayes	2005	1998-1999	Retrospective	(6) Low intensity – <30%-<26 yr; >60%->55 yr (5) Moderate. intensity – 40-60%-<26 yr; 40-60%->55 yr (5) High intensity – ≥60%-<26 yr; ≤30%->55 yr	E OR Coast Range btw Nestucca & Siuslaw R	Yes 3-tier	Yes	NA
Ashton et al	2006	2000-2001	Retrospective	(6) Mid-seral forests	Humboldt Co, NW CA	No	Yes	(6) Late-seral forests
Dupuis and Friele	2006	2001-2003	Retrospective	(156) Flathead streams (80) Yahk streams	Flathead & Yahk systems, SE BC	Yes 2-tier	Yes	NA

Table 3 (continued). Characteristics of studies linked to addressing potential effects of forestry practices on tailed frogs in the Pacific Northwest. Ng indicates values not given. In the Strata column, yes indicates one level, where more than one level existed, the number of tiers is show immediately below. In the Reference(s) column, pr indicates a pseudo-reference; one with a critical spatial or temporal confound.

Author(s)	Year		Study Characteristics					
	Publish	Executed	Type	Treatment(s) (# in parens)	Sampling Frame	Strata	Replication	Reference(s) (# in parens)
Hayes et al.	2006	2000-2005	Retrospective	(25) 1st-order basins (26) 2nd-order basins (13) 3rd-order basins (1) 4th-order basin	Stillman Basin SW WA	Yes	Yes	NA
Jackson et al.	2007	1998-2001	Manipulative	(6) Clearcut (4) Clearcut w buffers	WA Coast Range	Yes	Yes	(4) Unharvested
Olson and Rugger Olson and Weaver	2007 2007	1995-2002	Manipulative	(12) Thinned – multiple sampling units w/in treatments	Central W OR	Yes	Yes	(12) Unthinned – multiple sampling units w/in treatments
Kroll et al.	2008	2006	Retrospective	(141) 1st- to 3rd-order streams	Central W WA to Central W OR	No	Yes	NA
Kroll et al.	2010	2007-2008	Retrospective	(70) 3rd-order basins	Central Coastal OR to SW WA	No	Yes	NA
Pollett et al.	2010	2001	Retrospective	(12) Buffered clearcut (10) Unbuffered clearcut (10) 2nd-growth	W Cascades in S WA	Yes	Yes	(9) Unharvested
Hawkes and Gregory	2012	2003-2004	Manipulative	(6) State buffers (6) Modified buffers	SW WA SW WA Cascades	Yes	Yes	(6) Unharvested

Table 4. Significance and limitation of studies linked to addressing potential effects of forestry practices on tailed frogs in the Pacific Northwest. NA indicates condition is not applicable. US indicates condition was unspecified.

Author(s)	Year	Potential Limitations						Key Results or Findings
		Random Selection in Sampling Frame	Random Selection in Strata	Pseudo-replicated Units	Limited Sample Size (Power)	Detectability Addressed	Other	
Aho	1976	No	NA	NA	Yes	No	Case study	Initial suggestion of positive response for instream vertebrates (in this case cutthroat trout) from harvest induced increase in light levels
Murphy and Hall	1981	No	No	No	Yes	No	Potential spatial autocorrelation	Instream predator diversity was greater in clearcut reaches still exposed than in old-growth but this difference was lost with canopy regrowth
Murphy et al.	1981	US	No	No	Yes	No	Potential spatial autocorrelation	Streams in open clearcuts had greater microbial respiration, and greater densities and biomasses of aufwuchs, benthos, drift, salamanders and trout than shaded forested streams (within the relatively limited range of stream substrate categories examined)
Hawkins et al	1983	US	No	No	Yes	No	—	Salamander densities decreased as fine sediment increased among shaded streams, but open (low shade) streams showed no such relationship. Mechanism thought to be greater light increasing stream primary production that can masks the negative effects of more fine sediment
Bury	1983	US	NA	No	Yes	No	One *A. truei* capture	Abundance and biomass of amphibians greater in old-growth vs harvested plots
Hawkins et al	1988	US	Us	No	Yes	No	Temporal sampling confounds	Low larval *A. truei* densities appear most closely related to heavy stream substrate embeddedness and complete loss of watershed forest
Bury and Corn	1988a	No	Yes	No	Yes	No	Temporal issues with using pitfall trapping for abundance estimates	Species richness did not differ across the forest age gradient. Coastal tailed frog abundance not significantly different across either the forest age gradient or the moisture gradient in old-growth.

Table 4 (continued). Significance and limitation of studies linked to addressing potential effects of forestry practices on tailed frogs in the Pacific Northwest. NA indicates condition is not applicable. US indicates condition was unspecified.

Author(s)	Year	Potential Limitations						Key Results or Findings
		Random Selection in Sampling Frame	Random Selection in Strata	Pseudo-replicated Units	Limited Sample Size (Power)	Detectability Addressed	Other	
Corn and Bury	1989	US	NA	No	No	Partly	Size of sampling reach potentially influenced occupancy and abundance estimates	Coastal tailed frogs occurred more often in streams in harvested stands when uncut forest was present upstream but neither density nor biomass were related to either presence of uncut forest upstream or years since harvest
Welsh	1990	US	No	No	Yes	No	Size of sampling reach potentially influenced occupancy and abundance estimates	Coastal tailed frog abundance increased with forest age for sites <1000 m (3,280 ft) in elevation, and declined sharply in streams <1000 m in elevation with water temperatures ≥15 C (59 F)
Corn and Bury	1991	US	No	No	No	No	Temporal issues with using pitfall trapping for abundance estimates	Coastal tailed frogs were most abundant in wet stands on a moisture gradient in old-growth; no significant difference was found in Coastal tailed abundance with a stand age gradient
Gilbert and Allwine	1991	US	No	No	No	No	Temporal issues with using pitfall trapping for abundance estimates	Coastal tailed frog was significantly more abundant at the northern end of a latitudinal gradient, Coastal tailed frog appeared to shift toward old-growth at the southern end of this gradient and away from old-growth at the north end of this gradient.
Aubry and Hall	1991	US	No	No	No	No	Temporal issues with using pitfall trapping for abundance estimates	Coastal tailed frog was significantly more abundant in mature stands than either old-growth or young stands; no significant differences were observed in Coastal tailed frog across an old-growth moisture gradient

Table 4 (continued). Significance and limitation of studies linked to addressing potential effects of forestry practices on tailed frogs in the Pacific Northwest. NA indicates condition is not applicable. US indicates condition was unspecified.

Author(s)	Year	Potential Limitations						Key Results or Findings
		Random Selection in Sampling Frame	Random Selection in Strata	Pseudo-replicated Units	Limited Sample Size (Power)	Detectability Addressed	Other	
Bury et al.	1991	US	No	No	No	No	Temporal issues with using pitfall trapping for abundance estimates	Repeats key results for Coastal tailed frog from Aubry and Hall (1991), Corn and Bury (1991), and Gilbert and Allwine (1991)
Lamberti et al.	1992	US	Yes	Yes	Yes	No	—	Experiment II:Algal biomass generally declined with increasing larval *A. truei* density; benthic chlorophyll a was also inversely related to tadpole density
Lamberti et al.	1992	US	Yes	No	Yes	No	High variability among streams w/in catchment types	Experiment III: Catchment type (headwater forested, forested, or unforested) did not appear to affect grazing levels in treatment (reduced tadpole grazing) vs control platforms (ambient grazing).
Lamberti et al.	1992	US	Yes	Yes	Yes	No	Case study	Experiment IV: Treatment platforms (reduced tadpole grazing) in the headwater-forested stream were about 50 times higher in algal biomass and six times higher in chlorophyll than control platforms (ambient grazing) than the same difference in their corresponding counterparts in the stream lacking forest
Kelsey	1995	US	Yes	No	Yes	Partly	Several sites unoccupied or unusable; high between-site variability	No significant difference in 2nd-yr *A. truei* abundance among harvested and unharvested treatments
Bull and Carter	1996a	No	No	No	Yes	No	—	No significant differences in abundance of Rocky Mountain tailed frog larvae and adults among three harvest categories

Table 4 (continued). Significance and limitation of studies linked to addressing potential effects of forestry practices on tailed frogs in the Pacific Northwest. NA indicates condition is not applicable. US indicates condition was unspecified.

Author(s)	Year	Potential Limitations						Key Results or Findings
		Random Selection in Sampling Frame	Random Selection in Strata	Pseudo-replicated Units	Limited Sample Size (Power)	Detectability Addressed	Other	
Richardson and Neill	1995 1998	No	No	No	No	No	—	Coastal tailed frog densities in clearcuts were significantly greater than in second-growth stands; larval coastal tailed frog occupancy showed no relationship with forest age
Welsh and Ollivier	1998	No	NA	Yes	Yes	No	Asymmetry bias in treatment unit size	Road-impacted streams more sedimented and embedded
Diller and Wallace	1999	Yes	NA	No	No	No	—	Unconsolidated substrates *A. truei*-unoccupied
Dupuis and Steventon	1999	US	US	No	No	No	—	*A. truei* larval densities were significantly lower in harvested than in buffered or old-growth creeks; densities decreased with increasing levels of fine sediment
Kelsey (in O'Connell et al.)	2000	No	Yes	No	Yes	Partly	Five sites unoccupied by *A. truei*	No significant difference in 2nd-yr *A. truei* larval abundance among harvest treatment; post-hoc power analysis indicates 100 sites needed to detect a treatment effect
Maxcy	2000	No	No	No	Yes	No	Too few *A. truei* post-metamorphs at three of six sites for comparison	One control site increased in *A. truei* captures from pre- to post-harvest; another control site and one buffered site decreased pre- to post-harvest
Aubry	2000	No	No	No	Yes	No	Too few *A. truei* post-metamorphs for robust comparison	Nine of only 15 post-metamorphic *A. truei* found were recorded in the pre-canopy (12=20 yr) forest category
Wilkins and Peterson	2000	Yes	Yes	No	Yes	No	Few *A. truei*-occupied sites	Only basalt substrates appeared *A. truei*-occupied and abundance; abundance of amphibians generally greater on basalt than marine sedimentary substrates

Table 4 (continued). Significance and limitation of studies linked to addressing potential effects of forestry practices on tailed frogs in the Pacific Northwest. NA indicates condition is not applicable. US indicates condition was unspecified.

Author(s)	Year	Potential Limitations						Key Results or Findings
		Random Selection in Sampling Frame	Random Selection in Strata	Pseudo-replicated Units	Limited Sample Size (Power)	Detectability Addressed	Other	
Wahbe and Bunnell	2001	US	Yes	No	Yes	No	—	Coastal tailed frog larvae average movements 7.4× further in unmanaged forests than in clearcuts
Kiffney and Richardson	2001	No	Yes	No	Yes	No	—	Coastal tailed frog larvae in nutrient supplemented channels had growth rates four times higher than unsupplemented controls; insect grazer abundance in channels was lower in the presence of *A. truei* larvae regardless of nutrient supplementation, but the reduction was greater in nutrient-enriched channels
Adams and Bury	2002	No	No	Yes	No	No	—	Coastal tailed frog densities (all life stages combined) showed a strong positive relationship to elevation, a strong negative relationship to aspect in degrees from north, and a strong but complex bimodal relationship to gradient; Coastal tailed was also found to occupy unconsolidated lithologies at higher frequencies than reported in other studies
Wahbe and Bunnell	2003	US	Yes	No	Yes	No	High among site variability	Density, biomass, and body size were greatest in streams flowing through old-growth, but forest harvest effects were strongly modulated by site characteristics; over 86% of variation in density and biomass was associated with site-specific characteristics
Mallory and Richardson	2005	US	Yes	No	No	No	Pronounced differences between sites	Light has a strong positive effect on algae and periphyton production over shaded treatments, and consequently, on *A. truei* growth rates; algae and periphyton were under simultaneous top-down (tadpole grazing) and bottom-up (control), but relative importance of these effects was stream-dependent

Table 4 (continued). Significance and limitation of studies linked to addressing potential effects of forestry practices on tailed frogs in the Pacific Northwest. NA indicates condition is not applicable. US indicates condition was unspecified.

Author(s)	Year	Potential Limitations						Key Results or Findings
		Random Selection in Sampling Frame	Random Selection in Strata	Pseudo-replicated Units	Limited Sample Size (Power)	Detectability Addressed	Other	
Matsuda and Richardson	2005	US	Yes	No	Yes	No	Temporal issues with using pitfall trapping for abundance estimates	Total frog abundance was similar in clearcuts and mature forest; more adults were caught in mature stands than clearcuts but number of juveniles did not differ significantly between the two; variation among sites had a greater influence on juvenile numbers than habitat type
Stoddard and Hayes	2005	Yes	Yes	Yes	No	No	—	At the drainage and intermediate scales, *A. truei* was positively associated with reaches with RMZs >46 m (151 ft) wide; at the 2-m unit scale, *A. truei* was negatively associated with the amount of fine substrate
Ashton et al	2006	No	No	No	No	No	Asymmetry bias in treatment unit size	Amphibian species richness and densities of post metamorphic *A. truei* are significantly greater in late seral than managed mid-seral forests.
Dupuis and Friele	2006	Yes	Yes	Yes	No	No	—	Peak *A. montanus* occupancy and abundance at intermediate but relatively small basin sizes
Hayes et al.	2006	Yes	Yes	No	No	No	—	No reproductive occupancy in 1st-order basins linked to limited perennially watered reach length in those basins
Jackson et al.	2007	No	Yes	No	Yes	No	10 unoccupied sites forced evaluation as case studies	Coastal tailed frogs were detected in only five stream (3 clearcut, 1 reference, and 1 buffered); immediately after harvest; Coastal tailed frogs went undetected in all three clearcut streams, but appeared in one of the three streams one year later. In the buffered and reference stream, tailed frogs were present pre- and post-harvest
Olson and Rugger Olson and Weaver	2007 2007	No	Yes	Yes	No	No	Spatial autocorrelation	No significant difference between thinned and unthinned treatments, including *A. truei*

Table 4 (continued). Significance and limitation of studies linked to addressing potential effects of forestry practices on tailed frogs in the Pacific Northwest. NA indicates condition is not applicable. US indicates condition was unspecified.

Author(s)	Year	Potential Limitations						Key Results or Findings
		Random Selection in Sampling Frame	Random Selection in Strata	Pseudo-replicated Units	Limited Sample Size (Power)	Detectability Addressed	Other	
Kroll et al.	2008	Yes	Yes	No	No	Yes	—	Coastal tailed frog probability of occupancy increased with stream size peaking at a relatively small intermediate size (4 m bankfull width) and declined thereafter; and also increased with stand age (across the 70-80 year age range found in managed forest); Coastal tailed frog probability of occupancy was depressed by crayfish regardless of other conditions
Kroll et al.	2010	Yes	Yes	No	No	Yes	—	Coastal tailed frog probability of occupancy averaged 0.6 in western Oregon and southwest Washington, but varied substantially geographically, being highest in the Cascades of SW Washington and lowest in the Willapa Hills. Coastal tailed frog species detection probabilities were estimated at 0.86 (95% confidence intervals: 0.67-0.95)
Pollett et al.	2010	No	No	No	No	No	—	Coastal tailed frog densities were two-seven fold lower in streams in managed forests and in streams in unharvested forests. In addition, Coastal tailed frog was
Hawkes and Gregory	2010	No	No	No	Yes	No	Temporal issues with using pitfall trapping for abundance estimates	Post-metamorphic Coastal tailed frog densities declined 2-10 years post-harvest

of mistranslation, misinterpretation and uncritical generalizations that extends as far back as the first observations of Gaige (1920) appears to color the perspective of at least some investigators. Fewer than 10 years ago, Ashton and colleagues (2006) stated that "..harvested-related habitat alterations have been shown to negatively impact populations of *A. truei* in ***most*** regions of the PNW.." (emboldened italics ours). Specifically, Ashton and colleagues (2006) cited five studies (Bury 1983, Corn and Bury 1989, Kelsey 1994, Bull and Carter 1996a, Dupuis and Stevenson 1999) to support that contention. Of these five, only Corn and Bury (1989) and Dupuis and Steventon (1999) demonstrated a significant negative effect on *A. truei*, but in both cases, inference may be limited because both used single-pass sampling that involved a 10-m reach in the case of Corn and Bury (1989) and three 5-m reaches in the case of Dupuis and Steventon (1999). As for the other three studies: Bury (1983) had but a single data point for *A. truei*; Kelsey (1994) is a conference abstract preceding her dissertation (Kelsey 1995; see also Kelsey 2000), in which she could find no significant differences between harvest treatments in two studies that became, by unfortunate circumstances, reduced in *A. truei*-occupied replicates (see pages 36 and 106), and for which she determined, using power analysis, that 100 sites would have been needed to discern treatment effects; and Bull and Carter (1996a) studied *A. montanus*, not *A. truei*, but their analysis revealed no significant harvest effects even after adjusting for outliers in their analysis. Misinterpretation notwithstanding, a series of important conclusions are readily drawn from this review:

1) **A riparian management zone (RMZ) or buffer appears to have a positive effect on *A. truei* occupancy or abundance**. The most robust retrospective studies (e.g., Stoddard and Hayes 2005, Pollett et al. 2010) suggest this pattern, and no studies to date have shown that RMZs have a negative effect. Given tailed frogs are forest-adapted taxa, this result should not be surprising. RMZs can mitigate some of the negative responses associated with clear-cut harvests (Corn and Bury 1989) or clear-cut harvest and different RMZ treatments (Dupuis and Steventon, Jackson et al. 2007). We view this conclusion conditional because a positive buffer effect, or the degree of protection provided by RMZs is likely regionally specific (see conclusion 3) and species detectability remains an overarching problem in these studies (see conclusion 8).

2) **Timber harvest effects on tailed frogs, where they have been identified, are equivocal and complex and based on weak inference**. Weak inference results from a consequence of retrospective study designs that assumed pre-treatment abundance or occupancy patterns were similar across treatments or equivalent across the landscape (see Corn and Bury 1989, Welsh 1990, Bull and Carter 1996a, Dupuis and Steventon 1999, Stoddard and Hayes 2005, Ashton et al. 2006), limited replication in the case of the few manipulative studies that was sometimes outside of the control of the investigators (Kelsey 1995, 2000, Jackson et al. 2007), and no consideration of tailed frog detectability across treatments (see conclusion 8; see also Kroll [2009] for a discussion of some of these issues). In one instance, a post-hoc power analysis revealed that variability was too great, given estimates of effect size distinguish among treatments (Kelsey 1995). Several additional problems, discussed previously, dilute the strength of studies. Many studies include non-random or unknown landscape-level sampling frame that make generalizations of study results ambiguous (the majority of studies to date; see Table 4). Others suffer from pseudoreplication (e.g., Stoddard and Hayes 2005, Olson and Rugger

2007, Olson and Weaver 2007; see Table 4) that artificially inflates the true number of replicates, or biases in site selection that favor one treatment site category over another (see Welsh and Ollivier 1998, Ashton *et al.* 2006).

Nonetheless, lack of robust data are not support for lack of effects, the potential negative responses highlighted by selected studies indicate that a refocus of the response variable measured may be required. Kroll and colleagues (2008, 2010) have clearly demonstrated that Coastal tailed frog is broadly distributed on the managed landscape, but tailed frog abundance responses to forestry practices, where detectability-corrected abundance has been measured, remains unaddressed. Naïve abundance estimates indicating that Coastal frog numbers dropped to zero in three clearcut treatments when buffered and unharvested treatments did not (Jackson *et al.* 2007); that densities were 2-7 fold lower in managed than in unmanaged forests (Pollett *et al.* 2010); and that clearcut treatments were uniformily low relative to buffered and unharvested treatments (Maxcy 2000) suggest such a measure would be worthwhile. Moreover, given naïve abundance estimates for *A. truei* remained at zero two years post-treatment in the study of Jackson and colleagues (2007), a study that measures detectability-corrected abundance over enough of a time interval to identify potential recovery would appear critical.

3) **Geographic location likely underlies important differences in how tailed frog populations respond to harvest**. This conclusion may seem obvious given the large (15.5°) latitudinal range over which *A. truei* is distributed (see DISTRIBUTION SUMMARY section, pages 14-15). However, this conclusion has also been poorly appreciated until Kiffney and Richardson (2001) showed in a manipulative study that primary productivity increased as a consequence of reduced shading - a suggestion that originated from the retrospective study of Hawkins and colleagues (1988). No study has specifically examined *A. truei* response to increased productivity across a broad latitudinal range. We believe that light availability uniformly increasing with southerly latitude over the north temperate landscape (Garg and Prakash 2000); the shift toward *A. truei* using light richer earlier seral stages at more northerly latitudes (Gilbert and Allwine 1991); and the above discussed studies revealing light limitation (e.g., Kiffney and Richardson 2001) having occurred at high latitudes suggests that a latitudinal gradient where light availability directly affects *A. truei* larval response is a working hypothesis that deserves study. For forestry practices, the importance of understanding this pattern is that the positive effects of shade reduction demonstrated for *A. truei* at higher latitudes are likely to differ with decreasing latitude, and as a result, may require different approaches to manage for tailed frogs across large latitudinal swaths. Moreover, Bury (1968) had originally suggested and Diller and Wallace (1999) later identified a coastal-inland gradient in *A. truei* response to forestry practices, but this has not been considered as a basis for forest management. Elevation gradients in tailed frog response should also be expected.

4) **Site-specific effects have been viewed as secondary in considering how tailed frogs respond to harvest treatments**. In the search focused on identifying harvest-linked treatment effects, site-specific effects have been almost invariably ignored, at least as part of any directly expected result. Yet, many studies have displayed inconsistencies that are difficult to explain without invoking such effects, and a number of investigators have lamented about the degree of site-specific variability (e.g., Lamberti et al 1992, Kelsey 1995, Wahbe and Bunnell 2003). The work of Mallory and Richardson (2005) illustrates

elegantly the way in which site-specific conditions can complicate both interactions and interpretation even in a tightly controlled manipulative design. In early studies, situations that might arise from site-specific effects were often not discussed in that context, such as the unanticipated lack of correlation between larval *A. truei* density and water temperatures identified by Hawkins and colleagues (1988). When Welsh (1990) posed the questioned of why the patterns of tailed frog abundance were not more strongly associated with forest age, his response was that forest age was but an indirect measure of limiting factors, and that microhabitat or microclimate features that varied in parallel with forest age were the real limiting factors. Microhabitats and microclimates typically exhibit high variability among sites, so his statement implies that site-specific influences may be basic in explaining his rather noisy correlation. Similarly, Bull and Carter (1996*a*) suggested that stream characteristics were more important than landscape characteristics in predicting *A. montanus* abundance. Matsuda and Richardson (2005) even made the suggestion that site-specific effects may exceed treatment effects in magnitude. If this is the case, studies addressing tailed frogs intended to identify forestry practices effects must address site-specific variation to minimize potentially substantial confounds.

5) **Studies of forestry practices have addressed the effects of harvest *per se* on tailed frogs to the near exclusion of other forestry practices**. For example, road building, which typically precedes harvest on most units, is well known to produce severe sedimentation where road engineering had little attention (Rice *et al*. 1979, Reid and Dunne 1984), but has been studies on amphibians largely outside the Pacific Northwest (de Maynadier and Hunter 1995, 2000; Gibbs 1998). Only one study, that of Welsh and Ollivier (1998), has addressed road construction-associated sedimentation on a tailed frog (in this case *A. truei*), but that study addressed effects during construction of a four-lane highway, not a harvest unit road, which typically barely exceeds one lane in width. Further, engineering of forest roads expressly for the purpose of limiting sedimentation has improved dramatically over the last 20 years (Luce and Black 1999, 2001; Lugo and Gucinski 2000, Gucinski *et al*. 2001, Rhee *et al*. 2004). Sedimentation effects on any stream-associated amphibian under the current way forest roads are engineered are unstudied and unique challenges exist to the study of sedimentation effects (see conclusion 6). Further, other forestry practices, such as fertilizer applications to enhance tree growth or herbicide applications to reduce brush that may compete with young trees, are largely unstudied in the field for their potential effects on stream-associated amphibians like tailed frogs (see Spromberg and Birge 2005, McComb et al. 2008, Bruhl et al. 2011).

6) **The negative effect of sedimentation on stream-associated amphibians remains poorly understood.** Sediment that fills interstitial spaces in the streambed matrix, based on the hypothesis suggested by Corn and Bury (1989), is thought to be the detrimental aspect of harvest activities to tailed frogs. However, the precise effects of sedimentation on tailed frogs is an unexplored "black box" for which only the presumed output result of the effects have been identified (e.g., see Welsh and Ollivier 1998). Immobile egg masses and quasi-sedentary hatchling *Ascaphus* larvae may not survive a sedimentation episode, and a fine sediment layer may limit the access of older larvae to their diatom-dominated food in the "aufwuchs" film on rock surfaces (see LIFE HISTORY section for details), but

direct examination of mechanisms that produce mortality or reduce fitness are lacking. Few fine sediments may be needed to affect detectability (see conclusion 8), so how this may affect evaluating tailed frog response to sedimentation is unclear. Lastly, at least one study (i.e., Bull and Carter 1996*a*) showed a positive relationship between finer sediment and *A. montanus* abundance, but whether this relationship is spurious due to detectability problems or little sediment actually results in a positive effect based on an unrecognized mechanism for this tailed frog species is unknown.

7) **Studies of tailed frog have focused on the larval stage**. Most studies that address tailed frogs have used daytime sampling, but the post-metamorphic life stages of tailed frogs seem predominantly night active (see LIFE HISTORY section). Of the few studies that have focused on post-metamorphic life stages, all involved at least some sampling at night (see Daugherty and Sheldon 1982a, 1982b; Ashton *et al.* 2006; Burkholder and Diller 2007, Jones 2008), but only one of these (Ashton *et al.* 2006) has addressed forestry practices. Given the greater spatial and temporal variability in numbers of the larval stages of stillwater-breeding amphibians than their post-metamorphic counterparts (Turner 1962, Berven 1990), why one would assume that the larvae of stream-associated amphibians are less variable is not clear. Variability is unquestionably a concern for many reasons beyond life stage differences, and post-metamorphic life stages (particularly adults) provide a much more direct way to estimate population sizes, so it is difficult to understand why juveniles and adults are not sampled beyond ease of daytime sampling, which represents the time at which one can most successfully sample larvae. If one were to estimate population responses of a stillwater-breeding species exclusively demographically (versus genetically) from larval data, the approach might be questioned.

8) **Addressing species and individual detectabilities is a non-trivial problem that can alter results.** Detectability did not emerge as a concept needing attention until recently largely because either it was assumed to be high enough to not contribute substantially to variation in species occupancies or abundances or that it did not change under different conditions. Corn and Bury (1989) were the first to address detectability in some form for PNW stream-associated amphibians by estimating the rate at which they underestimated occupancy (false negative error rate) for *A. truei* in their 10-m sample reaches. However, their method of estimating detectability, which was designed to determine whether one 10-m reach was adequate to detect amphibian species presence, was based on use of only three 10-m reaches 50 m apart in the same stream. Further, *A. truei* had been determined *a priori* to be present in that stream. Hence, capability for generalization from the false negative error rate they determined is limited because the test of their method was limited to an extraordinarily small, non-random subset of the forested condition under which they applied the method.[368] More important, they reported abundance data, but the probability of detecting individual *A. truei*, the parameter required to adjust abundance estimates when the probability of detecting individuals is less than 1, was not determined. Since all estimates of the mean probability of detecting individual tailed frogs that we know of are

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[368] Corn and Bury (1989) described their test as addressing the ability of our method to characterize abundance, but their analysis was based on binomial probabilities in which they determined *p*, the proportion of 1-m segments in a 10-m reach in which the species was present, which does not characterize abundance. They defined their estimated Type I error as the binomial probability of capturing no *A. truei* in 10 1-m segments. They recognized that they probably underestimated Type I error because they did not randomly select their 1-m segments. Their test was done on three 10-reaches 50 m apart on the South Fork of the Smith River, Douglas County, Oregon.

≤0.81 (A. McIntyre, *unpublished data*; J. MacCracken, *personal communication*), the abundances that Corn and Bury (1989) obtained are underestimates that varied with detectability-influenced covariates in manner that reconstructing them is not possible. Similarly, Kelsey (1995) calculated the probability of not detecting *A. truei* given the total number of 10-m segments surveyed.[369] However, because her study also estimated abundance without adjusting for the detectability of individual tailed frogs, her estimates are undoubtedly low in a way that cannot be reconstructed as well. Emerging recognition that species detectabilities are far enough below 1 to alter estimates of occupancy in a significant way, that detectabilities vary with diverse covariates (Kroll et al. 2008), and that individual detectabilities for amphibians may typically be rather low (Bailey et al. 2004) has drawn attention to the importance of incorporating detectability into estimates for both occupancy and abundance. Most important, if detectability changes greatly with a changing covariate as a direct consequence of a treatment application, e.g., a harvest treatment, failure to estimate the change in detectability pre- versus post-harvest could alter study results. This idea casts a shadow over previous studies because the alternatives between addressing detectabilities or have the potential to change results in a manner that conclusions may be reversed.

9) **Studies addressing the differences between the two tailed frog species are needed to properly interpret their responses in studies focused on forestry practices effects.** Indications that differences may exist in larvae temperature requirements (Adams and Frissell 2001, Dunham et al. 2007) were the first indication of fundamental differences in ecology of the two tailed frog species. This was followed by potential differences in larvae distribution (Jones 2008) and genetic data that suggested potentially significant differences how gene flow may occur (Spear and Storfer 2010). Collectively, these data suggest that comparative information on temperature requirements for all life stages, movement patterns, and genetics need to be available to effectively interpret manipulative studies on forestry practices that may be implemented for *A. montanus*. To date, the only study addressing forestry practices on *A. montanus* is the retrospective study of Bull and Carter (1996a).

10) **Comparative studies between managed and unmanaged landscapes remain a gap.** Historically, resistance has existed to conducting studies contrasting managed and unmanaged landscapes, likely based on concern about timber industry image, but a few a comparative studies between these landscapes have begun to emerge (see Ashton *et al.* 2006, Pollett *et al.* 2010). However, Kroll and colleagues (2008, 2010) have shown that Coastal tailed frogs occur across the managed landscape in a manner more broadly distributed than heretofore recognized. Moreover, Kroll and colleagues (2010) expressly pointed out that the high occurrence probabilities for stream-associated amphibians, including Coastal tailed frog, found on the managed landscape reflect one of three possibilities: 1) the extirpation of stream-associated amphibians from previous occupied basins (assuming 100% occupancy, this would be loss from an average of 40% of basins for Coastal tailed frog); 2) static occupancy over time; or 3) increases in occupancy probabilities. They further point out that without comparable data from unmanaged

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[369] Because streams were sampled in two or three areas, Kelsey (1995) randomly selected either the first, second, or third survey and counted the number of surveys without *A. truei*. This process was repeated 10 times and a mean proportion of surveys without *A. truei* to total surveys was calculated.

forests or data collected sometime prior to harvest on the sites they sampled, which of these possibilities is most likely cannot be addressed. We add that such studies would also be critical to understanding process-based differences between managed and unmanaged landscape and would be particularly important to execute over gradients where we anticipate that process differences may be manifest (see conclusion 3). That kind of understanding is critical to tailoring the best forestry management practices to the regional conditions.

11) **Sampling techniques have evolved and will continue to evolve.** Earlier studies that did not address detectability (see conclusion 8 and Table 4) were focused on techniques that were thought to maximize catchability, but these were done under the assumption that the numbers of animals detected were insignificant enough to not affect results. With the incorporation of detectability into estimates, which requires sampling involving at least two passes, understanding the detectability of alternative techniques (Quinn *et al.* 2007) that have never been evaluated for detectability is crucial, especially if comparison among studies is considered. Recently, Cossel and colleagues (2012) recently compared detection using electrofishing to the rubble-rousing method (see Quinn et al. 2007) for Idaho giant salamanders (*Dicamptodon aterrimus*). With rubble-rousing, they detected *D. aterrimus* in 12 of 20 25-m reaches (detection rate = 0.60), but detected salamanders on all 20 segments using electrofishing. With rubble-rousing, they detected *A. montanus* at 14 of 25 sites (detection rate = 0.56); with electrofishing, their detection probability was 0.79 (95% CI = 0.63-0.88). They concluded that electrofishing was a more sensitive method than rubble rousing for detecting stream-amphibians, but other considerations might mitigate its use.

CLIMATE CHANGE IN THE RANGE OF TAILED FROGS

Marc Hayes

The emergence of climate change from being a somewhat controversial hypothesis in the 1990s to a reality manifest as tangible global-level changes in the last 15 years made it important to consider how climate change might influence tailed frogs. Climate change in the PNW will result in a number of direct and indirect threats to tailed frogs that have the potential to dwarf the effects of all other environmental factors. Direct effects generally include increasing air and water temperatures, and changes to the timing, variability, and form (rain versus snow) of precipitation (Lawler and Mathias 2007, Lawler *et al.* 2008). Global temperatures have increased 0.74°C (1.33°F)[370] on average over the century 1906 to 2005, and are predicted to increase of an additional 1.1-6.4°C [2.0-11.5°F][371] by 2100; IPCC 2007). Climate change over the past century has altered the phenology of plant growth and migration timing, and caused shifts in species distributions, but changes over the next decades are anticipated to be even more dramatic (Lawler and Mathias 2007, Lawler *et al.* 2008).

Climatic change affects physical systems, which in turn affect biological systems. The physical systems most likely to influence tailed frogs are the cryosphere (ice, snow, and

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[370] Ninety-five percent confidence interval 0.54-0.92°C (0.97-1.66°F).

[371] Range of warming projections reflects both model scenarios and a large range of models of varying complexity (IPCC 2007).

frozen ground) and hydrological systems. The array of tailed frog responses to these systems is diverse, especially because complex secondary effects may occur that are anticipated to be difficult to predict.[372] Hence, only the important and least speculative changes are summarized here.

Accumulated winter snow in montane watersheds contributes most streamflow runoff in western North America and similar regions of the world (Grant and Kahan 1974, Mote *et al.* 2005). In a warmer world, less winter precipitation falls as snow (Barnett *et al.* 2005). Over the 20th century, the PNW has warmed by an average of about 0.8°C (1.5°F)[373] (Mote 2003a) and perhaps the foremost impact of this warming has been a declining snowpack. The PNW has sustained a 16% decline in snow cover[374] over the interval 1950-2003 (Groisman *et al.* 2001, 2004) and declines in mountain snow water equivalents[375] at about 75% of locations monitored (Mote 2003b, Mote *et al.* 2005). Further, the prediction from climate models is that additional warming of 0.5-2.5°C (0.9-4.5°F; central estimate 1.5°C [2.7°F]) is anticipated by the 2020s, and 1.5°-3.2°C (2.7-5.8°F; central estimate 2.3°C [4.1°F]) by the 2040s (Mote *et al.* 2003). These predictions make almost certain that the declining snowpack trend will continue (Lapp *et al.* 2005) along with earlier spring thaws (Cayan *et al.* 2001) and increases in stream temperatures. Coupled to the observed increases in air temperature are increases in annual precipitation, particularly in winter (Mote *et al.* 2003) with more of that precipitation falling as rain rather than snow, a phenomenon especially evident in the PNW, where winter temperatures are already relatively close to the melting point of ice and snow (Regonda *et al.* 2005). Extreme precipitation events have contributed disproportionately to these increases (Karl and Knight 1998, Groisman *et al.* 2001). Since logging can alter the hydrological regimes (Wright et al. 1990, Hicks et al. 1991, Jones and Grant 1996, Jones and Post 2004), interaction with precipitation predictions for climate change, which are predicted to have effects that may or may not be parallel, need to be understood.

The most direct effect of climate change may just be a temperature effect. Stenothermic species may be locally extirpated as thermally appropriate habitat vanishes (Hauer *et al.* 1998). For *A. truei*, arguably the most cool stenothermic of North American frogs (see LIFE HISTORY), the negative effect of warming could result in loss of oviposition sites where stream temperatures reach 18.5°C [65.3°F] critical thermal maximum (CTM) that kills early embryonic stages. We anticipate that streams most vulnerable to climate change would have one or more of the following characteristics, including:

1) located toward the southern end of the geographic range;
2) located at low elevations;
3) located in interior (non-coastal) streams;
4) located on south-facing slopes;
5) have low stream discharge;

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[372] A substantial amount uncertainty in making confident predictions is the major gaps in understanding tailed frog ecology (see LIFE HISTORY section).

[373] Selected weather stations have reported cooling trends over this period, but most stations show warming over the last century (Mote 2003a). Further, cooling trends are far weaker and less significant than the majority of the warming trends over this period (Mote 2003a).

[374] Estimate based on the percentage change over a 100 years (Groisman *et al.* 2004).

[375] Snow water equivalents (SWE), a common snowpack measurement, is the amount of water contained within the snowpack. It can be thought of as the volume of water that would theoretically result if one melted the entire snowpack instantaneously.

6) located in streams with few cold water refugia; and
7) have a rainwater-dependent hydrology.

All these conditions are associated with streams with a greater likelihood of having elevated water temperatures regardless of climate change. Tailed frogs may undergo latitudinal and elevational shifts with warming, as has been reported for other species (Hickling *et al.* 2006). If the CTM for *A. truei*, obtained from a northern Washington population, is similar throughout its geographic range, then we might expect a similar response from *A. montanus* despite that fact that it may have a higher CMT (see Life History section). Nonetheless, the already warmer continental climate in which *A. montanus* occurs is expected to sustain greater absolute changes in temperature with climate warming (Mote *et al*. 2005), so at some point, *A. montanus* will be vulnerable to elevated temperatures. At landscape and watershed scales, warming temperatures may increasingly isolate cooler-adapted water taxa to progressively smaller headwater areas (Hauer *et al.* 1998). Where watersheds are small, as occurs in near-coastal western Washington, the area to which tailed frogs may be confined may ultimately become too small to maintain viable populations.

Additionally, it needs emphasis that CTM data may be a poor predictor of changes over the short-term if stress temperatures for tailed frogs exist that are well below their CTMs. Given that *A. truei* occupancy suggests relatively rarity in streams with summertime temperatures in the 15°C range or above, some reason exists to expect this possibility. This means that determining stress temperatures will be critical in evaluating responses that may be observed over the short-term, otherwise, local extirpations could occur and go unrecognized.

The coming decades are expected to see an increase in the proportion of rain-based winter precipitation, an increase in the frequency of winter high-water events, continued reduction in snowpack, and an increase in winter streamflows that result in earlier peak flows (Stewart *et al.* 2005) and decreased late spring and summer flows (Lawler and Mathias 2008).

These predictions are consistent with observed rates and directions of change during the past 50 years. Moreover, the greatest changes are expected to occur in the PNW, Sierra Nevada, and Rocky Mountains, where many rivers are projected to eventually run 30–40 days earlier by 2100 (Stewart *et al*. 2004). Because winter temperatures are closer to the melting point of ice/snow in the PNW, more precipitation as rain resulting from modest upward shifts in temperature is capable of translating into a large shifts in hydrological response (Regonda *et al*. 2005).[376]

The summer hydrology will change as well. While the PNW is anticipated to become wetter overall, the projected increase is less than the range of decadal variability (Hamlet *et al.* 2005). Any small amount of additional summer precipitation is expected to be too little to overcome the drier summer season or mitigate the decreased soil moisture caused

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[376] Earlier modeling of hydrological changes in streams in south-central British Columbia due to projected climate change by Leith and Whitfield (1998) was in strong agreement. In late autumn and early winter, higher temperatures would result in more precipitation as rain rather than snow, resulting in a modest increase in rainfall runoff during this period. These higher late-autumn/early-winter streamflows would result in earlier spring runoff and a reduced streamflow in the subsequent summer months.

by elevated temperatures (Hamlet and Lettenmaier 1999). These patterns have a number of possible consequences for tailed frogs; the more important are:

1) Historical oviposition sites may become increasingly unreliable if water flow is insufficient during the period of early development or if smaller flows increase the possibilities of water temperatures reaching stressfull levels or the CTM.
2) Decreased summer flows may result in historically perennial stream becoming spatially intermittent or drying out altogether (see Hunter *et al*. 2005). Drying may force aquatic life stages into perennial reaches that have more predators.
3) Decreased soil moisture may be insufficient to provide non-aquatic refuges for adults (see Hayes *et al*. 2006).
4) Decreased summer flows and spatial intermittency may reduce invertebrate production upon which tailed frogs depend (see Hayes *et al.* 2006).
5) Increased winter high water events may increase the likelihood of debris flows, which appears to represent the dominant substrate movement mechanism in headwater reaches (Brummer and Montgomery 2003), where tailed frogs occur. Debris flows that are too frequent could reduce or eliminate entire cohorts of the aquatic life stages (see LIFE HISTORY section).

Climate change scenarios predict greater temperatures changes in continental locations, but the effect of those changes on *A. montanus* is unclear in context of recent work on the species (Dunham *et al.* 2007, Spear and Storfer 2010). Regardless of which species of tailed frog, however, we anticipate that populations at more southerly latitudes, on east slopes and low elevations may be more affected by decreases in summer flows and soil moisture than populations at more northerly latitudes, on west slopes, and at higher elevations.

Warming, decreased soil moisture, and earlier spring thaw will increase wildfire activity in western US forests (Westerling *et al.* 2006). Wildfire activity increased suddenly and markedly in the mid-1980s, with more frequent large wildfires, longer-lasting wildfires, and longer wildfire seasons. Though increases in wildfire activity has been a general pattern across the west, the greatest increases have occurred in mid-elevation northern Rocky Mountain forests, where land-use histories have contributed relatively little to fire risk and increases in wildfire activity are strongly associated with the increase in the already higher continental temperatures in spring and summer and earlier spring snowmelt (Westerling *et al.* 2006). For example, as of the review by Hossack and Pilliod (2011), 23.9% of the entire geographic range of *A. montanus* has been burned since 1987; parallel data are not available for *A. truei*. Despite the recent call for information on fire effects on amphibians (Pilliod *et al.* 2003), information addressing tailed frogs remains sparse. Increased fire frequency in northern Rocky Mountain forests has resulted in the few studies to date addressing *A. montanus*. Based on assessment of larvae pre- and post-fire (Hossack and Corn 2005), *A. montanus* persisted following fire in one study in Glacier National Park, but likely at close to half the density found in unburned reference streams[377] (Hossack *et al.* 2006). Fire seemed to have the greatest negative effect on abundance of 1st-year larvae, but the basis of that effect was not understood. Hossack (2006) also commented that larvae on burned sites with south-facing slopes seemed more

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[377] Pre-fire counts were similar in 4 burned and 4 unburned (reference) streams (Hossack *et al.* 2006).

vulnerable, but the basis of that vulnerability was not specified. Dunham and colleagues (2007), who studied streams with contrasting wildfire and physical disturbance histories,[378] found no differences in occupancy of *A. montanus* larvae between streams exposed and not exposed to burning. Moreover, as previously noted, *A. montanus* occurred at nearly every site sampled, regardless of water temperatures. Low-stature (short) riparian vegetation did not seem to prevent stream heating in their study streams. However, streams affecting by burning were not as warm as those that were burned and reorganized with little riparian vegetation, which suggests that recovered streamside vegetation in burned streams provides important shading. Most recently, Spear and Storfer (2010) showed that fire appeared to have little effect on gene flow. To date, wildfire studies on *A. montanus* provide relatively little evidence to suggest negative effects, and none of each of Hossack and colleagues (2006), Dunham and colleagues (2007), and Spear and Storfer (2010) viewed fire as an extirpation threat in the streams they sampled. Understanding the effects of more frequent or widespread fires on *A. montanus* will likely require studies spanning a chronosequence of fires and conditions (Hossack *et al.* 2006, Dunham *et al.* 2007, Hossack and Pilliod 2011).

Hauer and colleagues (1998) suggest that climate change could alter riparian vegetation. Changes in riparian assemblages may in turn affect tailed frog refuge sites, possibly via aquatic habitat warming (see Dunham et al. 2007) or food resources. However, we know so little about tailed frog ecology with regard to riparian assemblage dynamics that it is not possible to make even basic predictions about possible effects.

Focal to conservation is elucidating how climate change may interact with management actions, like forestry practices, to affect persistence of tailed frogs. Unfortunately, large uncertainties exist about the effects of climate change especially at local spatial scales, so uncertainties regarding interactive effects with forestry practices are high as well.

FUTURE DIRECTIONS

This review underscores the fact that existing science can only provide general guidance to conserving or maintaining tailed frogs on managed forestlands. Below we summarize significant knowledge gaps.

Climate Change: The emerging and accelerating environmental changes resulting from climate change will create changing baselines that will render results of many previous studies increasingly less pertinent and repeatable through time. As a result studies that address how climate change might interact with forest practices to affect tailed frogs should be among the highest priority for continuing adaptive management efforts. We suggest considering the following lines of work:

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[378] Dunham and colleagues (2007) compared thermal variability of streams in three major disturbance categories: streams without recent stand-replacing wildfire in their watersheds; streams with a recent history of moderate-to-high-severity wildfire predominant in the watershed; and streams in watersheds with a recent history of moderate-high severity wildfire that had massive channel reorganization from a debris flow or flood. This analysis was complemented with long-term information from a collection of samples over 3-13 years that contrasted pre- and post-fire temperatures in burned and unburned streams. They also examined the distribution of two focal species in the coldwater guild of aquatic vertebrates (rainbow trout and Rocky Mountain tailed frog) among sites and streams to determine if observed temperature changes associated with wildfire influenced species occurrence.

1) Field experiments should determine whether water temperature changes as a consequence of harvest impact tailed frogs. Some of these experiments should determine the spatial and temporal patterns of groundwater inputs and hyporheic flows, and how these patterns may influence tailed frog ecology. To have predictive utility, especially for climate change, some experiments should have breath in latitude, longitude, or elevation because stream temperatures are known to vary, often substantially, along these gradients. Other experiments should include temperature variation as a function of stream hydrology in tailed frog-occupied streams. The magnitude of water temperature fluctuations is known to be linked to flow volume and water source. Understandng how habitat use changes with water temperature or flow fluctuations is critical since many permanent headwater streams may be shifting to a spatially intermittent form.
2) As with temperature, field experiments should be developed to determine how harvest-related changes in stream flow may affect different tailed frog life stages. Experiments should focus on prescriptions most likely to increase, decrease, or change the magnitude and variation in stream flows. Similar to experiments addressing harvest-related temperature changes, these experiments should include examination of the environmental gradients (e.g., basin area, precipitation) known to affect flow.
3) Conduct field experiments addressing before-versus-after-harvest changes in the quality (moisture and temperature) of adult tailed frog refuge sites. Fieldwork that develops a basic understanding of adult tailed frog refuge sites during different seasons may need to precede such experiments.
4) Comparative studies between managed and unmanaged landscapes, as mentioned earlier, will be needed to identify process shifts that may occur between managed and unmanaged landscapes in a climate change context, especially if they occur differently between landscapes.

Other Key Gaps in a Forest Practices Context: This represents important information gaps about how tailed frogs may respond in a current forest practices context.

1) As discussed earlier, forest practices rules in Washington currently require a RMZ over at least 50 percent of the stream length in headwater (Type N) streams. Effectiveness of this length of RMZ for *A. truei* is currently unknown, but will be addressed, at least in part, by the Type N Experimental Buffer Treatment Study on Hard Rock Lithologies, a manipulative landscape-study site that includes *A. truei* that addresses the effective of this buffer prescription in Washington State.
2) Forest practices rules in Washington also require a 15.2 m (50 ft) RMZ on both sides of the stream. The importance of addressing RMZ width and length is related to the tradeoff in habitat quality for tailed frogs. If primarily productivity of headwater streams are light limited as discussed earlier, then increasing RMZ decreases primary productivity but may help maintain cool stream temperatures, while decreasing RMZ width increases primary productivity and may raise stream temperatures. Further, it would seem important to understand how this tradeoff may change with latitude and in the context of climate change.

3) Forest practice rules in Washington prescribe a 15.2 m (50 ft) management zone for five categories of sensitive sites (alluvial fans, headwall seeps, headwater springs, side-slope seep, and tributary junctions; WFPB 2001), but the value of protecting these sensitive sites has not been evaluated for either species of tailed frog. The Type N study in Washington will provide some data on the value of at least two of these sensitive site categories (headwater springs and tributary junctions) to *A. truei*.
4) Forest practices rules in Washington prescribe a 15.2 m (50 ft) RMZ on both sides of the stream regardless of the side-slope gradient. Streams with higher gradient side-slopes are more vulnerable to colluvial input, so higher gradient side-slopes may require a particular RMZ prescription to accommodate tailed frogs. Unstable slide slopes are typically covered under another part the unstable slope rules.
5) Comparative studies between managed and unmanaged are also important outside of a climate change context, in part for evaluating the occupancy reasons indicated by Kroll and colleagues (2010), and in part to address hypotheses regarding differences in occupancy and abundance in low gradient or sedimentary lithology landscapes and how those may change over latitudinal, longitudinal, or elevation gradients (e.g., Adams and Bury 2002).

Fundamental Life History Knowledge Gaps: This represents gaps in knowledge of tailed frog life history that make it difficult to interpret tailed frog responses to forest practices.

1) Laboratory experiments to gain a fundamental understanding of variation in CTMs or stress temperatures for various life stages of both tailed frog species is basic to understanding temperature-associated risks, especially selected studies addressing climate change. Emphasis should be placed on response of various tailed frog life stages to stress temperatures because animals typically do not, at least intentionally, exposure themselves to temperatures at the level of CTMs. Some experiments should establish whether geographic variation exists in stress temperature thresholds across both tailed frog species, and what alternative conditions (e.g., temperature acclimatization, alternative stressors) can modulate those thresholds.
2) Data on the life history of post-metamorphic life stages of both species of tailed frog are notably inadequate. In particular, we need more information in two areas: a) the seasonal movement patterns of juveniles and adults; and b) overwintering habitat of these life stages. Movement data are especially important because adult *A. truei* use or travel through portions of headwater basins that typically lack a RMZ under current headwater (Type N) stream prescriptions in Washington.
3) Research on the effects of large logjams on larva*l Ascaphus* movement (Wahbe and Bunnell 2001) had ambiguous result. Woody debris could conceivably hinder movement but is also can stabilize step pool stream morphology, which is important habitat feature for tailed frogs. in certain headwater streams.
4) We need a more sophisticated examination of the substrate size distributions associated with high quality habitat for all life stages of tailed frogs, especially because different life stages likely prefer different substrate sizes, so an idealized

mix of sizes is likely to maximize recruitment and survival.

5) We need to better understand the relationship between tailed frogs and lithology. Lithologies that do not produce large clast inorganic substrates may be limiting, but examining this possibility is difficult because tailed frog occupied basins are often not lithologically uniform.
6) Overland movements information by post-metamorphic life stages in context of seasonal patterns is perhaps the most glaring gap in current understanding of tailed frog life history, especially in context of physical or biotic conditions that trigger movement because potential changes in those conditions from diverse factors, including forestry practices, is what is critical to understand in order to take actions that should be taken to manage for tailed frogs.
7) Much better understanding of biophysical gradients (temperature, light, slope, aspect, primary productivity, nutrient limitation, seasonality of discharge) that affect tailed frogs across latitudinal, longitudinal, and elevational gradients to be able to predict changes and inform management options.
8) Quantitative population capture-mark-recapture that allow for rigorous estimation of population growth rates, individual trajectories of body condition, and body size (size structure) are needed. Population-level inference is nearly absent from the current published literature on tailed frogs, so such studies have the potential to provide the basis for broader inference on diverse aspects of tailed frog response to habitat changes, including ones associated with forestry practices.
9) This review did not address disease at any level, Hossack and colleagues (2010) examined 492 tailed frogs across their geographic ranges and found a very low prevalence of the amphibian chytrid fungus, *Batrachochytrium dendrobatidis*. This represents a baseline study that suggests that this disease, which is responsible for decline and extinction of a number of amphibians globally does not appear to be a problem at this point. However, given the rapid expansion of this disease globally, follow-up studies would be well justified, particular to understand potential interactions with climate change and forestry practices.

General Conditions that Need Attention: These are general conditions that investigators should consider *a priori* in tailed frog investigations.

1) Given the need to reduce variation in population and species occupancy estimates, incorporating variation in detectability in a sensible way should be basic to all field studies. The Type N Hard Rock Study and potential other studies near completion will clarify some of this perspective, but a number of variables affecting species detection have yet to be identified and understood.
2) Experiments should be conducted with the intent of evaluating the effectiveness of actual forest practices rules. That is, forest practices as they are now conducted across the geographic ranges of both tailed frog species, not conditions that are historic, or rare or non-existent under current rules.
3) Given variability in field experiments, we believe it is time to do more simulated stream studies in test channels (similar to that of Mallory and Richardson 2005)

where sediment inputs, temperature and light can be manipulated while effectively limiting variation on other variables. Critically, such experiments need sensible coupling to field conditions and experiments.

4) More attention should be given to addressing effect size in planning for major field studies via pilot studies of some kind. Pilot studies can use approaches such as that recommended by Di Stefano (2004) for contrasting effect sizes and treatment effects.

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LITERATURE CITED

Abourachid, A. and D.M. Green. 1999. Origins of the frog-kick? Alternate-leg swimming in primitive frogs, families Leiopelmatidae and Ascaphidae. Journal of Herpetology 33(4):657-663.

Adams, M.J. 1993. Summer nests of the tailed frog (*Ascaphus truei*) from the Oregon coast range. Northwestern Naturalist 74(1):15-18.

Adams, M.J. 2014. Personal communication to M. Hayes, 14 October 2014.

Adams, M.J., and R. B. Bury. 2000. Association of stream amphibians with climate gradients and the characteristics of headwater streams. Pp. 25-31 *In*: Bury, R.B., and M.J. Adams (editors), Inventory and Monitoring of Amphibians in North Cascades and Olympic National Parks, 1995-1998. Final Report, Forest & Rangeland Ecosystem Science Center in Cooperation with Olympic National Park, US Department of Interior and US Geological Survey, Corvallis, Oregon, USA.

Adams, M.J., and R.B. Bury. 2002. The endemic headwater stream amphibians of the

American Northwest: associations with environmental gradients in a large forested preserve. Global Ecology and Biogeography 11:169-178.

Adams, M.J. and C.A. Pearl. 2005a. Part Two - Species Accounts: *Ascaphus truei*. Pp. 382-384. *In*: Lannoo, M.J. (editor), Status and Conservation of U.S. Amphibians. University of California Press. Berkeley, California, USA.

Adams, M.J. and C.A. Pearl. 2005b. Part Two - Species Accounts: *Ascaphus montanus*. Pp. 382. *In*: Lannoo, M.J. (editor), Status and Conservation of U.S. Amphibians. University of California Press. Berkeley, California, USA.

Adams, M.J. and A.G. Wilson Jr. 1993. Geographic distribution. *Ascaphus truei*. Herpetological Review 24(2):64.

Adams, S.B., and C.A. Frissell. 2001. Thermal habitat use and evidence of seasonal migration by Rocky Mountain Tailed Frogs, *Ascaphus montanus*, in Montana. Canadian Field-Naturalist 115(2):251-256.

Aho, R.S. 1976. A population study of cutthroat trout in an unshaded and shaded section of stream. MSc thesis, Department of Wildlife and Fisheries, Oregon State University, Corvallis, Oregon, USA. 87 p.

Aitkin, K. 2011. Personal communication to M. Hayes, 4 April.

Altig, R. and E.D. Brodie, Jr. 1972. Laboratory behavior of tailed frog *Ascaphus truei* tadpoles. Journal of Herpetology 6(1):21-24.

Altig, R. and A. Channing. 1993. Hypothesis: Functional significance of colour and pattern of anuran tadpoles. Herpetological Journal 3(2):73-75.

Anderson, G.A., and I. Pratt. 1965. Cercaria and first intermediate host of *Euryhelmis squamula*. Journal of Parasitology 51(1):13-15.

Anderson, G.A., S.C. Schell, and I. Pratt. 1965. The life cycle of *Bunoderella metteri* (Allocreadiidae: Bunoderinae), a trematode parasite of *Ascaphus truei*. Journal of Parasitology 51(4):579-582.

Anderson, G.A., G.W. Martin, and I. Pratt. 1966. The life cycle of the trematode *Cephalouterina dicamptodoni* Senger and Macy, 1953. Journal of Parasitology 52(4):704-706.

Anderson, P.D., D.J. Larson, and S.S. Chan. 2007. Riparian buffer and density management influences on microclimate of young headwater forests of western Oregon. Forest Science 53(x):254–269.

Arnold, S.J., and R.J. Wassersug. 1978. Differential predation on metamorphic anurans by garter snakes (*Thamnophis*): Social behavior as a possible defense. Ecology 59(5):1014-1022.

Asay, M.J., and S.K. Boyd. 2000. Distribution of arginine vasotocin in the brain of a non-vocalizing anuran (*Ascaphus truei*). American Zoologist 40(6):932. [abstract]

Ashton, D.T., S.B. Marks, and H. H. Welsh, Jr. 2006. Evidence of continued effects from timber harvesting on lotic amphibians in redwood forests of northwestern California. Forest Ecology and Management 221(1-3):183–193.

Aubry, K.B. 1997. Influence of stand structure and landscape composition on terrestrial amphibians. Pp. 1-43 *In*: Aubry, K.B., S.D. West, D.A. Manuwal, A.B. Stringer, J.L. Erickson, and S. Pearson (editors), Wildlife Use of Managed Forests: A Landscape Perspective. Volume 2. West-side Studies Research Results. USDA Forest Service.

Aubry, K.B. 2000. Amphibians in managed, second-growth Douglas-fir forests. Journal of Wildlife Management 64(4):1041-1052.

Aubry, K.B. and P.A. Hall. 1991. Terrestrial amphibian communities in the southern Washington Cascade Range. Pp. 327-338. *In*: Ruggiero, L.F., K.B. Aubry, A.B. Carey and M.H. Huff (editors), Wildlife and Vegetation of Unmanaged Douglas-fir Forests. USFS Pacific Northwest Research Station. PNW-GTR-285, Olympia, Washington, USA.

Aubry, K.B., C.B. Halpern, and D.A. Maguire. 2004. Ecological effects of variable retention harvests in the northwestern United States: the DEMO study. Forests, Snow and Landscape Research 78(1/2):119-137.

Bailey, L.L., T.R. Simons, and K.H. Pollock. 2004. Estimating site occupancy and species detection probability parameters for terrestrial salamanders. Ecological Applications 14(3):692-702.

Barnett, T.P., J.C. Adam, and D.P. Lettenmaier. 2005. Potential impacts of a warming climate on water availability in snow-dominated regions. Nature 438:303-309.

Beers, T.W., P.E. Dress, and L.C. Wensel. 1966. Aspect transformation on site productivity research. Journal of Forestry 64:691-692

Belton, J.C. and A. Owczarzak. 1968. Cellular changes associated with pre-ovulatory deposition and storage of hepatic lipids in the frog *Ascaphus truei*. Herpetologica 24(2):113-127.

Benda, L.E. 1990. The influence of debris flows on channels and valley floors in the Oregon Coast Range, USA. Earth Surface Processes and Landforms 15(5):457-466.

Berven, K.A. 1981. Mate choice in the wood frog, *Rana sylvatica*. Evolution 35(4):707-722.

Berven, Keith A. 1990. Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). Ecology 71(4):1599–1608.

Beschta, M. 1978. Long-term patterns of sediment production following road construction and logging in the Oregon Coast Range. Water Resources Research 14(6):1011-1016.

Beschta, R.L., R.E. Bilby, G.W. Brown, L.B. Holtby, and T.D. Hofstra. 1987. Stream temperatures and aquatic habitat: Fisheries and forestry interactions, Pp. 191-232. *In*: E.O. Salo and T.W. Cundy (editors), Streamside management: Forestry and fishery interactions. Contribution No. 57, Institute of Forest Resources, University of

Washington, Seattle.

Blair, J. and R.J. Wassersug. 2000. Variation in the pattern of predator-induced damage to tadpole tails. Copeia 2000(2):390-401.

Bogart, J.P., E.K. Balon, and M.N. Bruton. 1994. The chromosomes of the living coelacanth and their remarkable similarity to those of one of the most ancient frogs. Journal of Heredity 85(4):322-325.

Bondar, C.A., K. Bottriell, K. Zeron, and J.S. Richardson. 2005. Does trophic position of the omnivorous signal crayfish (*Pacifastacus leniusculus*) in a stream food web vary with life history stage or density? Canadian Journal of Fisheries and Aquatic Sciences 62(11):2632-2639.

Bosakowski, T. 1999. Amphibian macrohabitat associations on a private industrial forest in western Washington. Northwestern Naturalist 80(2):61-69.

Bridges, C.M., and R.D. Semlitsch. 2000. Variation in pesticide tolerance of tadpoles among and within species of Ranidae and patterns of amphibian decline. Conservation Biology 14(5):1490-1499.

Bridges, C.M. 2000. Long-term effects of pesticide exposure at various life stages of the southern leopard frog (*Rana sphenocephala*). Archives of Environmental Contamination and Toxicology 39(1):91-96.

BCCDC [British Columbia Conservation Data Centre]. 2014. British Columbia Species and Ecosystems Explorer. British Columbia Ministry of Environment, Victoria, British Columbia, Canada. (http://a100.gov.bc.ca/pub/eswp/, accessed 13 November 2014)

British Columbia Ministry of Forests and British Columbia Ministry of Environment, Lands and Parks. 1995*a*. Biodiversity Guidebook. Forest Practices Code of British Columbia. Ministry of Forests and Ministry of Environment, Lands and Parks, Victoria, British Columbia, Canada.

British Columbia Ministry of Forests and British Columbia Ministry of Environment, Lands and Parks. 1995*b*. Riparian Management Area Guidebook. Forest Practices Code of British Columbia. Ministry of Forests and Ministry of Environment, Lands and Parks, Victoria, British Columbia, Canada.

British Columbia Ministry of Forests and British Columbia Ministry of Environment, Lands and Parks. 1995*c*. Forest Road Engineering Guidebook. Forest Practices Code of British Columbia. Ministry of Forests and Ministry of Environment, Lands and Parks, Victoria, British Columbia, Canada.

British Columbia Ministry of Forests and British Columbia Ministry of Environment, Lands and Parks. 1999. Managing Identified Wildlife: Procedures and Measures. Forest Practices Code of British Columbia. Volume I. Ministry of Forests and Ministry of Environment, Lands and Parks, Victoria, British Columbia, Canada.

Brown, G.W., and J.T. Krygier. 1970. Effects of clear-cutting on stream temperatures. Water Resources Research 6(4):1133-1139.

Brown, H.A. 1975. Temperature and development of the tailed frog, *Ascaphus truei*. Comparative Biochemistry and Physiology 50A(2):397-405.

Brown, H.A. 1989. Developmental anatomy of the tailed frog (*Ascaphus truei*): a primitive frog with large eggs and slow development. Journal of Zoology (London) 217(4):525-537.

Brown, H.A. 1990. Morphological variation and age-class determination in overwintering tadpoles of the tailed frog, *Ascaphus truei*. Journal of Zoology (London) 220(2):171-184.

Brown, H.A. 2005. Coastal tailed frog – *Ascaphus truei*, Pp. 154-157. *In*: Jones, L.L.C., W.P. Leonard, and D.H. Olson (editors), Amphibians of the Pacific Northwest. Seattle Audubon Society, Seattle, Washington, USA.

Brown, L.R., and Jason T. May. 2007. Aquatic vertebrate assemblages of the upper Clear Creek watershed, California. Western North American Naturalist 67(3):439-451.

Bruhl, C.A., S. Pieper, and B. Weber. 2011. Amphibians at risk? Susceptibility of terrestrial amphibian life stages to pesticides. Environmental Toxicology and Chemistry 30(11):2465-2472.

Brummer, C.J. and D.R. Montgomery. 2003. Downstream coarsening in headwater channels. Water Resources Research 39(10):1294-1307.

Bull, E.L. 1994b. Effect of logging on tailed frog populations in northeastern Oregon. Northwest Science 68(2):117.

Bull, E.L. and B.E. Carter. 1996*a*. Tailed frogs: distribution, ecology, and association with timber harvest in northeastern Oregon. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA. PNW-RP-497.

Bull, E.L. and B.E. Carter. 1996*b*. Winter observations of tailed frogs in northeastern Oregon. Northwestern Naturalist 77(2):45-47.

Bunnell, F.L. and L.A. Dupuis. 1995. Riparian habitats in British Columbia; their nature and role. Pp. 7-21 *In*: Morgan, K.H. and M.A. Lashmar (editors). Conference Proceedings. Riparian Habitat Management and Research. Fraser River Action Plan, Environment Canada, and the Canadian Wildlife Service, Kamloops, British Columbia, Canada.

Burkholder, L.L., and L.V. Diller. 2007. Life history of post-metamorphic Coastal Tailed Frogs (*Ascaphus truei*) in northwestern California. Journal of Herpetology 41(2):251-262.

Bury, R.B. 1968. The distribution of *Ascaphus truei* in California. Herpetologica 24(1):39-46.

Bury, R.B. 1970. Food similarities in the tailed frog, *Ascaphus truei*, and the Olympic salamander, *Rhyacotriton olympicus*. Copeia 1970(1):170-171.

Bury, R.B. 1983. Differences in amphibian populations in logged and old-growth redwood forest. Northwest Science 57(3):167-178.

Bury, R.B. 2008. Low thermal tolerances of stream amphibians in the Pacific Northwest: Implications for riparian and forest management. Applied Herpetology 5(1):63-74.

Bury, R.B. 2014. Personal communication to M. Hayes, 6 October 2014.

Bury, R.B. and M.J. Adams. 1999. Variation in age at metamorphosis across a latitudinal gradient for the tailed frog, *Ascaphus truei*. Herpetologica 55(2):283-291.

Bury, R.B. and P.S. Corn 1987. Evaluation of pitfall trapping in northwestern forests: trap arrays with drift fences. Journal of Wildlife Management 51(1):112-119.

Bury, R.B. and P.S. Corn. 1988*a*. Douglas-fir forests in the Oregon and Washington Cascades: relation of the herpetofauna to stand age and moisture. Pp. 11-22. *In*: Szaro, R.C., K.E. Severson and D.R. Patton (technical coordinators). Management of Amphibians, Reptiles and Small Mammals in North America. USFS Rocky Mountain Forest and Range Experiment Station. GTR-RM-166. Flagstaff, Arizona, USA.

Bury, R.B. and P.S. Corn. 1988*b*. Responses of aquatic and streamside amphibians to timber harvest: a review. Pp. 165-181. *In*: Raedeke, K.J. (editor), Streamside management: riparian wildlife and forestry interactions: Proceedings of a symposium; 1987 Feb. 11-13; Institute of Forest Resources, University of Washington, Seattle, Washington, USA. Contribution 59.

Bury, R.B. and P.S. Corn. 1991. Sampling methods for amphibians in streams in the Pacific Northwest. USDA Forest Service. Portland, Oregon, USA. General Technical Report. PNW-GTR-275.

Bury, R.B., G.M. Fellers, and S.B. Ruth. 1969. First records of *Plethodon dunni* in California, and new distributional data on *Ascaphus truei*, *Rhyacotriton olympicus*, and *Hydromantes shastae*. Journal of Herpetology 3(3-4):157-161.

Bury, R.B, P.S. Corn and K.B. Aubry 1991*a*. Regional patterns of terrestrial amphibian communities in Oregon and Washington. Pp. 341-350. *In*: Ruggiero, L.F., K.B. Aubry, A.B. Carey and M.H. Huff (editors), Wildlife and Vegetation of Unmanaged Douglas-fir Forests. USFS Pacific Northwest Research Station. PNW-GTR-285, Olympia, Washington, USA.

Bury, R.B., P.S. Corn, K.B. Aubry, F.F. Gilbert and L.L.C. Jones. 1991*b*. Aquatic amphibian communities in Oregon and Washington. Pp. 353-362. *In*: Ruggiero, L.F., K.B. Aubry, A.B. Carey and M.H. Huff (editors), Wildlife and Vegetation of Unmanaged Douglas-fir Forests. USFS Pacific Northwest Research Station. PNW-GTR-285, Olympia, Washington, USA.

Bury, R.B., P. Loafman, D. Rofkar, and K.I. Mike. 2001. Clutch sizes and nests of tailed frogs from the Olympic Peninsula, Washington. Northwest Science 75(4):419-422.

Caldwell, J. P. 1982. Disruptive selection: A tail color polymorphism in *Acris* tadpoles in response to differential predation. Canadian Journal of Zoology 60(11):2818–2827.

CDFW [California Department of Fish and Wildlife] 2014. Special Animals List. Periodic Publication, California Natural Diversity Database, California Department of Fish and Game, Sacramento, California, USA. 52 p. [September] (http://www.dfg.ca.gov/biogeodata/cnddb/pdfs/SPAnimals.pdf, accessed 13 November 2014)

Camp, C.L. 1917. Another record for *Ascaphus truei* Stejneger. Copeia (40):13-14.

Carl, G.C., and I.M. Cowan. 1945. Notes on some frogs and toads of British Columbia. Copeia 1945(1):52-53.

Carl, G.C. 1949. Extension of known ranges of some amphibians in British Columbia. Herpetologica 5(6):139-140.

Carl, G.C. 1955. Northward extension of the known range of the Tailed Frog, *Ascaphus truei* Stejneger. Herpetologica 11(3):202.

Cayan, D.R., S.A. Kammerdiener, M.D. Dettinger, J.M. Caprio and D.H. Peterson. 2001. Changes in the onset of spring in the western United States. Bulletin of the American Meteorological Society 82(2):399-415.

Chen, J., S.C. Saunders, T.R. Crow, R.J. Naiman, K.D. Brosofske, G.D. Mroz, B.L. Brookshire, and J.F. Franklin. 1999. Microclimate in forest ecosystem and landscape ecology. Bioscience 49(4):288-297.

Chin, A. 1989. Step-pools in stream channels. Progress in Physical Geography 13(3):391-408.

Clark, L.A., G.J. Roloff, V.L. Tatum, and L.L. Irwin. 2009. Forest herbicide effects on Pacific Northwest ecosystems: A literature review. National Council for Air and Stream Improvement, Inc., Research Triangle Park, North Carolina, Technical Bulletin No. 970. 64 pp.

Claussen, D.L. 1973a. The thermal relations of the tailed frog, *Ascaphus truei* and the Pacific treefrog, *Hyla regilla*. Comparative Biochemistry and Physiology 44**A**(1):137-153.

Claussen, D.L. 1973b. The water relations of the tailed frog, *Ascaphus truei* and the Pacific treefrog, *Hyla regilla*. Comparative Biochemistry and Physiology 44**A**(1):155-171.

Claussen, D.L. 1974. Water balance and jumping ability in anuran amphibians. American Zoologist 14(4):1257.

COSEWIC [Committee on the Status of Endangered Wildlife in Canada). 2011. COSEWIC assessment and status report on the Coastal Tailed Frog *Ascaphus truei*. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Canada. 53 p. (http://www.registrelep-sararegistry.gc.ca/default_e.cfm, accessed 13 November 2014)

COSEWIC [Committee on the Status of Endangered Wildlife in Canada). 2013. COSEWIC assessment and status report on the Rocky Mountain Tailed Frog *Ascaphus montanus*. Committee on the Status of Endangered Wildlife in Canada, Ottawa, Canada. 46 p. (http://www.registrelep-sararegistry.gc.ca/default_e.cfm, accessed 13 November 2014)

Conlon, J.M., A. Sonnevend, C. Davidson, D.D. Smith and P.F. Nielsen. 2004. The ascaphins: a family of antimicrobial peptides from the skin secretions of the most primitive extant frog, *Ascaphus truei*. Biochemical and Biophysical Research Communications 320(1):170-175.

Conlon, J.M., T. Jouenne, P. Cosette, D. Cosquer, H. Vaudry, C.K. Taylor and P.W. Abel. 2005. Bradykinin-related peptides and tryptophyllins in the skin secretions of the most primitive extant frog, *Ascaphus truei*. General and Comparative Endocrinology 143(2):193-199.

Conlon, J.M., C.R. Bevier, L. Coquet, J. Leprince, T. Jouenne, H. Vaudry and B.R. Hossack. 2007. Peptidomic analysis of skin secretions supports separate species status for the tailed frogs, *Ascaphus truei* and *Ascaphus montanus*. Comparative Biochemistry and Physiology Part D: Genomics and Proteomics 2(2):121-125. [June]

Conservation Data Centre. 2001. Ministry of Environment, Lands and Parks. Victoria, British Columbia.

Corbit, C.D. 1960. Range extension of *Ascaphus truei* in Idaho. Copeia 1960(2):240.

Corkran, C. and C. Thoms. 2006. Amphibians of Oregon, Washington, and British Columbia, Revised and Updated. A Field Identification Guide. Lone Pine Publishing, Auburn, Washington, USA. 176 p.

Corn, P.S. and R.B. Bury. 1989. Logging in western Oregon: responses of headwater habitats and stream amphibians. Forest Ecology and Management 29(1):39-57.

Corn, P.S. and R.B. Bury. 1991. Terrestrial amphibian communities in the Oregon coast range. Pp. 341-350. *In*: Ruggiero, L.F., K.B. Aubry, A.B. Carey and M.H. Huff (editors), Wildlife and Vegetation of Unmanaged Douglas-fir Forests. USFS Pacific Northwest Research Station. PNW-GTR-285, Olympia, Washington, USA.

Cossel, J.O., M.G. Gauge, and J.D. Sauder. 2012. Electroshocking as a survey technique for stream-dwelling amphibians. Wildlife Society Bulletin 36(2):358-364.

Creed, R.P. 2006. Predator transitions in stream communities: A model and evidence from field studies. Journal of the North American Benthological Society 25(3):533-544.

Crisafulli, C.M. 2011. Personal communication to M. Hayes, 23 March.

Crisafulli, C.M. and C.P. Hawkins. 1998. Ecosystem recovery following catastrophic disturbance: Lessons learned from Mount St. Helens. *In*: Mac, M.J., P.A. Opler, C.E. Puckett Haecker, and P.D. Doran (editors), Status and Trends of the Nation's Biological Resources. U.S. Department of Interior, U.S. Geological Survey. Reston, Virginia, USA. Two Volumes, 964 p.

Crisafulli, C.M., L.S. Trippe, C.P. Hawkins, and J.A. MacMahon. 2005. Amphibian responses to the 1980 eruption of Mount St. Helens, Pp. 183-197. *In* Dale, V.H., F.J. Swanson, and C.M. Crisafulli (editors), Ecological responses to the 1980 eruption of Mount St. Helens, Springer-Verlag, New York, New York, USA.

Croke, J.C., and P.B. Hairsine. 2006. Sediment delivery in managed forests: A review. Environmental Reviews 14(1):59-87.

Crother, B.I. 2008. Scientific and Standard English Names of amphibians and reptiles of North America north of Mexico, with comments regarding confidence in our understanding, 6th edition. Herpetological Circular 37, Society for the Study of Amphibians and Reptiles. Salt Lake City, Utah, USA. 84 p.

Daugherty, C.H. 1979. Population ecology and genetics of *Ascaphus truei*: an examination of gene flow and natural selection. PhD Dissertation, University of Montana, Missoula, Montana, USA. 143 p.

Daugherty, C.H. and A.L. Sheldon. 1982*a*. Age-specific movement patterns of the frog *Ascaphus truei*. Herpetologica 38(4):468-474.

Daugherty, C.H. and A.L. Sheldon. 1982*b*. Age-determination, growth, and life history of a Montana population of the tailed frog (*Ascaphus truei*). Herpetologica 38(4):461-468.

Dawley, E.M. 1998. Olfaction, Pp. 711-742. In: H. Heatwole and E.M. Dawley, editors, Amphibian Biology, Volume III, Surrey Beatty & Sons, Chipping Norton, New South Wales, Australia.

de Maynadier, P.G., and M.L. Hunter, Jr. 2000. Road effects on amphibian movements in a forested landscape. Natural Areas Journal 20(1):56-65.

de Maynadier, P.G., and M.L. Hunter, Jr. 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. Environmental Reviews 3(3-4):230-261.

de Vlaming, V.L. and R.B. Bury 1970. Thermal selection in tadpoles of the Tailed-Frog, *Ascaphus truei*. Journal of Herpetology 4(3-4):179-189.

Deban, S.M. and K.C. Nishikawa. 1992. The kinematics of prey capture and the mechanism of tongue protraction in the green tree frog *Hyla cinerea*. Journal of Experimental Biology 170(1):235-256**.**

Dietrich, W.E., and T. Dunne. 1978. Sediment budget for a small catchment in mountainous terrain. Zeitschrift für Geomorphologie, Supplement 29:191-206.

Diller, L.V. and R.L. Wallace 1999. Distribution and habitat of *Ascaphus truei* in streams on managed, young growth forests in North Coastal California. Journal of Herpetology 33(1):71-79.

Di Stefano, J. 2004. A confidence interval approach to data analysis. Forest Ecology and Management 187:173–183.

Dodson, R. and D. Marks. 1997. Daily air temperature interpolated at high spatial resolution over a large mountainous region. Climate Research 8(1):1-20.

Donaldson, L.R. 1934. The occurrence of *Ascaphus truei* east of the continental divide. Copeia 1934(4):184.

Duellman, W.E. and L. Trueb. 1994. Biology of Amphibians. The Johns Hopkins University Press. Baltimore, Maryland, USA.

Dunham, J.B., A.E. Rosenberger, C.H. Luce, and B.E. Rieman. 2007. Influences of wildfire and channel reorganization on spatial and temporal variation in stream temperature and the distribution of fish and amphibians. Ecosystems 10(2):335-346.

Dupuis, L.A. 1998. The effect of various silvicultural treatments on amphibian assemblages of the Robert's Creek watershed. British Columbia Ministry of Forests, Vancouver, British Columbia, Canada. Interim Report.

Dupuis, L.A. 1999. Status Report on the Tailed Frog, *Ascaphus truei*, in Canada. COSEWIC report. 26 p.

Dupuis, L.A., and F.L. Bunnell. 1997. Status and distribution of the tailed frog in British Columbia. Centre for Applied Conservation Biology. Final Report for Forest Renewal British Columbia. 50 p.

Dupuis, L.A., and P.A. Friele. 1996. Riparian management and the tailed frog. Prince Rupert Forest Region. British Columbia, Ministry of Forests, Vancouver, British Columbia, Canada. Interim report. 18 p.

Dupuis, L.A., and P.A. Friele. 2006. The distribution of the Rocky Mountain tailed frog (*Ascaphus montanus*) in relation to the fluvial system: implications for management and conservation. Ecological Research 21(3):489-502.

Dupuis, L., and D. Steventon. 1999. Riparian management and the tailed frog in northern coastal forests. Forest Ecology and Management 124(1):35-43.

Dupuis, L., and K. Wilson. 1999. Status, distribution, and management needs of the tailed frog in the east Kootenays. British Columbia Ministry of Environment, Lands and Parks, Nelson, British Columbia, Canada. Unpublished Report. 19 p.

Dupuis, L.A., F.L. Bunnell, and P.A. Friele. 2000. Determinants of the tailed frog's range in British Columbia. Northwest Science 74(2):109-115.

Dvornich, K.M., K.R. McAllister, and K.B. Aubry. 1997. Amphibians and Reptiles of Washington State: Location data and predicted distributions, Volume 2: In Cassidy KM, Grue CE, Smith MR, Dvornich KM, editors. Washington State Gap Analysis-final report. Washington Cooperative Fish and Wildlife Research Unit, University of Washington, Seattle, Washington, USA. 304 p.

Feminella, J.W. and C.P. Hawkins. 1994. Tailed frog tadpoles differentially alter their feeding behavior in response to non-visual cues from four predators. Journal of the North American Benthological Society 13(2):310-320.

Ferguson, D.E. 1952. The distribution of amphibians and reptiles of Wallowa County, Oregon. Herpetologica 8(1):66-68.

Fitch, H.S. 1936. Amphibians and reptiles of the Rogue River Basin, Oregon. American Midland Naturalist 17(3):634-652.

FFR [Forests and Fish Report] 2000. Washington State Department of Natural Resources, Olympia, Washington, USA.

Forey, P.L. 1980. *Latimeria*: A paradoxical fish. Proceedings of the Royal Society of London, Series B, Biological Sciences 208(1172):369-384.

Fotheringham, A.S., C. Brunsdon, and M.E. Charlton. 2002. Geographic weighted regression: The analysis of spatially varying relationships. John Wiley & Sons, Ltd, Chichester, West Sussex, England.

Franklin, J.F.; F. Hall; W. Laudenslayer; C. Maser; J. Nunan; J. Poppino; C.J. Ralph; and T. Spies. 1986. Interim definitions for old growth Douglas-Fir and mixed-conifer forests in the Pacific Northwest and California, United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, Research Note PNW-447:1-7.

Franz, R. 1970*a*. Egg development of the tailed frog under natural conditions. Bulletin of the Maryland Herpetological Society 6(2):27-30.

Franz, R. 1970*b*. Food of larval tailed frogs. Bulletin of the Maryland Herpetological Society 6(3):49-51.

Franz, R. and D. Lee. 1970. The ecological and biogeorgraphical [*sic*] distribution of the tailed frog, *Ascaphus truei*, in the Flathead River drainage of northwestern Montana. Bulletin of the Maryland Herpetological Society 6(4):62-73.

Frost, D.R., T. Grant, J.N. Faivovich, R.H. Bain, A. Haas, Celio F.B. Haddad, R.O. de Sa, , A. Channings, M. Wilkinson, S.C. Donnellan, C.J. Raxworthy, J.A. Campbell, B.L. Blotto, P. Moler, R.C. Drewes, R.A. Nussbaum, J.D. Lynch, D.M. Green, and W.C. Wheeler. The amphibian tree of life. Bulletin of the American Museum of Natural History (297):1-370.

Gaige, H.T. 1920. Observations upon the habits of *Ascaphus truei* Stejneger. Occasional Papers of the Museum of Zoology, University of Michigan (84):1-11.

Gamradt, S.E., and L.B. Kats. 2002. Effect of introduced crayfish and mosquitofish on California newts. Conservation Biology 10(4):1155-1162.

Garg, H.P., and J. Prakash. 2000. Solar energy: Fundamentals and applications. Tata McGraw-Hill, New Delhi, India. 434 p.

Gibbs, J.P. 1998. Amphibian movements in response to forest edges, roads, and streambeds in southern New England. Journal of Wildlife Management 62(2):584-589.

Gilbert, F.F. and R. Allwine. 1991. Terrestrial amphibian communities in the Oregon Cascade Range. Pp. 319-326. *In*: Ruggiero, L.F., K.B. Aubry, A.B. Carey and M.H. Huff (editors), Wildlife and Vegetation of Unmanaged Douglas-fir Forests. USFS Pacific Northwest Research Station. PNW-GTR-285, Olympia, Washington, USA.

Gissi, C., D. San Mauro, G. Pezole, and R. Zardoya. 2006. Mitochondrial phylogeny of Anura (Amphibia): A case study of congruent phylogenetic reconstruction using amino acid and nucleotide characters. Gene 366:228-237.

Golliet, M. 2006. Using aquatic organisms as indicators of perennial stream flow. Northwestern Naturalist 87(2):169. [abstract]

Gomez, D.M. and R.G. Anthony 1996. Amphibian and reptile abundance in riparian and upslope areas of five forest types in western Oregon. Northwest Science 70(2):109-119.

Gorr, T., T. Kleinschmidt, and H. Fricke. 1991. Close tetrapod relationships of the coelacanth *Latimeria* indicated by haemoglobin sequences. Nature 351:394-397.

Govindarajulu, P.P. 2008. Literature review of impacts of glyphosate herbicide on amphibians: What risks can the silvicultural use of this herbicide pose for amphibians in British Columbia? Ministry of Environment, Victoria, British Columbia, Wildlife Report No. R-28. 79 pp.

Gradwell, N. 1971. *Ascaphus* tadpole: experiments on the suction and gill irrigation mechanism. Canadian Journal of Zoology 49(3):307-332.

Gradwell, N. 1973. On the functional morphology of suction and gill irrigation in the tadpole of *Ascaphus*, and notes on hibernation. Herpetologica 29(1):84-93.

Grant, J. 1961. The tailed toad in southeastern British Columbia. Canadian Field Naturalist 75(3):165.

Grant, G.E., F.J. Swanson, and M.G. Wolman. 1990. Pattern and origin of stepped-bed morphology in high-gradient streams, western Cascades, Oregon. Geological Society of America Bulletin 102(3):340-352.

Grant L.O. and A. M. Kahan. 1974. Weather modification for augmenting orographic precipitation, Pp. 282-317. *In*: W.N. Hess (editor), Weather and Climate Modification, John Wiley & Sons, Inc, Hoboken, New Jersey, USA.

Gray, L.A. 1992. Larval growth and age at completion of metamorphosis of the tailed frog, *Ascaphus truei*. MSc Thesis, Central Washington University, Ellensburg, Washington, USA. 62 p.

Green, D.M., C.H. Daugherty, and J.P. Bogart. 1980. Karyology and systematic relationships of the Tailed Frog *Ascaphus truei*. Herpetologica 36(4):346-352.

Green, D.M., T.F. Sharbel, R.A. Hitchmough, and C.H. Daugherty. 1989. Genetic variation in the genus *Leiopelma* and relationships to other primitive frogs. Zeitschrift für Zoologische Systematik und Evolutionsforschung 27(1):65-79.

Gregory, S.V., F.J. Swanson, W.A. McKee, and K.W. Cummins. 1991. An ecosystem perspective of riparian zones. Bioscience 41(8):540-551.

Grialou, J.A. West, S.D., and R.N. Wilkins. 2000. The effects of forest clearcut harvesting and thinning on terrestrial salamanders. Journal of Wildlife Management 64(1):105-113.

Grinnell, J., and C.L. Camp. 1917. A distributional list of the amphibians and reptiles of California. University of California Publications in Zoology 17(10):127-208.

Grizzel, J.D., and N. Wolff. 1998. Occurrence of windthrow in forest buffer strips and its effect on small streams in northwest Washington. Northwest Science 72:214 –223.

Groisman, P.Y., T.R. Karl and R.W. Knight, 1994. Observed impact of snow cover on the heat balance and the rise of continental spring temperatures. Science 263(5144):198–200.

Groisman, P.Y., R.W. Knight and T.R. Karl. 2001. Heavy precipitation and high streamflow in the contiguous United States: Trends in the 20th century. Bulletin of the American Meteorological Society 82(2):219–246.

Groisman, P.Y., R.W. Knight, T.R. Karl, D.R. Easterling, B. Sun, and J.H. Lawrimore. 2004. Contemporary changes of the hydrological cycle over the contiguous United States: Trends derived from in situ observations. Journal of Hydrometeorology 5(1):64–85.

Groves, C. 1994. Idaho's Amphibians and Reptiles. Non-game Wildlife Leaflet No. 7, Idaho Department of Fish and Game, Boise, Idaho, USA. 12 p.

Gunzburger, M.S., and J. Travis. 2005. Critical literature review of the evidence for unpalatability of amphibian eggs and larvae. Journal of Herpetology 39:547-571.

Gucinski, H., M.J. Furniss, R.R. Ziemer, and M.H. Brookes. 2001. Forest roads: A Synthesis of Scientific Information. US Department of Agriculture Forest Service Pacific Northwest Research Station, General Technical Report PNW GTR-509.

Gyug, L.W. 2001. Tailed Frog Inventory, Merritt Forest District: Project Report 2001. Okanagan Wildlife Consulting, Westbank, British Columbia, Canada. Prepared for British Columbia Ministry of Water, Land and Air Protection, Southern Interior Region, Kamloops, British Columbia, Canada. 30 p.

Haas, A. 2003. Phylogeny of frogs as inferred primarily from larval characters (Amphibian: Anura). Cladistics 19:23-89.

Haas, A., and S.J. Richards. 1998. Correlations of cranial morphology, ecology, and evolution in Australian suctorial tadpoles of the genera *Litoria* and *Nyctimystes* (Amphibia: Anura: Hylidae: Pelodryadinae). Journal of Morphology 238(2):109-141.

Hailman, J.P. 1982. Extremely low ambient light levels of *Ascaphus truei*. Journal of Herpetology 16(1):83-84.

Hailman, J.P., and R.G. Jaeger. 1976. A model of phototaxis and its evaluation in anuran amphibians. Behaviour 56(3-4):215-249.

Hall, J.D., and R.L. Lantz. 1969. Effects of logging on the habitat of coho salmon and cutthroat trout in coastal streams, Pp. 355-375. *In*: T.G. Northcote (editor), Symposium on salmon and trout in streams. University of British Columbia, Vancouver, British Columbia, Canada.

Hamlet, A.F. and D.P. Lettenmaier. 1999. Effects of climate change on hydrology and water resources in the Columbia River Basin. Journal of the American Water Resources Association 35(6):1597-1623.

Hamlet, A.F., P.W. Mote, M.P. Clark and D.P. Lettenmaier. 2005. Effects of temperature and precipitation variability on snowpack trends in the western United States. Journal of Climate 18(21):4545-4561.

Hankin, D.G., and G.H. Reeves. 1988. Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. Canadian Journal of Fisheries and Aquatic Sciences 45(5):834–844.

Hauer, F.R., J.S. Baron, D.H. Campbell, K.D. Fausch, S.W. Hostetler, G.H. Leavesley, P.R. Leavitt, D.M. McKnight and J.A. Stanford. 1998. Assessment of climate change and freshwater ecosystems of the Rocky Mountains, USA and Canada. Hydrological Processes 11(8):903-924.

Hawkes, V.C., and P.T. Gregory. 2012. Temporal changes in the relative abundance of amphibians relative to riparian buffer width in western Washington, USA. Forest Ecology and Management 274(1):67-80.

Hawkins, C.P., J. Feminella, and C.M. Crisafulli. 1997. Responses and recovery of stream-dwelling tailed frog and giant salamander populations following the 1980 eruption of Mount St. Helens. *In*: Richardson, J.S. and T.R. Wahbe (editors). Proceedings of the Tailed Frog Workshop. April 14-17, 1997. University of British Columbia. Vancouver, British Columbia, Canada. 49 p.

Hawkins, C.P., L.J. Gottschalk, and S.S. Brown. 1988. Densities and habitat of Tailed Frog tadpoles in small streams near Mt. St. Helens following the 1980 eruption. Journal of the North American Benthological Society 7(3):246-252.

Hawkins, C.P., M.L. Murphy, N.H. Anderson and M.A. Wilzbach. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. Canadian Journal of Fisheries and Aquatic Sciences. 40(8):1173-1185.

Hay, J.M., I. Ruvinsky, S.B. Hedges, and L.R. Maxson. 1995. Phylogenetic-relationships of amphibian families inferred from DNA-sequences of mitochondrial 12S and 16S ribosomal-RNA genes. Molecular Biology and Evolution 12(5):928-937.

Hayes, M.P. 1995. The amphibian and reptile fauna of the vicinity of the proposed Cherry Creek Research Natural Area. Report prepared for The Nature Conservancy as part of a cost-share agreement among the Bureau of Land Management, the Oregon Department of Fish and Wildlife, Pacificorp, the Weyerhaeuser Company, and the Winema National Forest. 20 p.

Hayes, M.P., T. Quinn, D.J. Dugger, T.L. Hicks, M. A. Melchiors, and D.E. Runde. 2006. Dispersion of Coastal Tailed Frog (*Ascaphus truei*): A hypothesis relating occurrence of frogs in non-fish-bearing headwater basins to their seasonal movement. Journal of Herpetology 40:533-545.

Held, S.P. 1985. Maintenance, exhibition, and breeding of the tailed frog, *Ascaphus truei*, in a zoological park. Herpetological Review 16(2):48-51.

Hertwig, S, R. O. de Sá, and A. Haas. 2008. Phylogenetic signal and the utility of 12S and 16S mtDNA in frog phylogeny. Journal of Zoological Systematics and Evolutionary Research 42(1):2-18.

Hickling, R., D.B. Roy, J.K. Hill, R. Fox, and C.D. Thomas. 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Global Change Biology 12(3):450-455.

Hicks, B.J., R.L. Beschta, and R.D. Harr. 1991. Long-term changes in streamflow following logging in western Oregon and associated fisheries implications. Water Resources Bulletin 28(2):217-226.

Hillman, S.S., P.C. Withers, and R.C. Drewes. 2000. Correlation of ventricle mass and dehydration tolerance in amphibians. Herpetologica 56(4):413-420.

Holland, R.S., 1976. Landforms of British Columbia: A physiographic outline. Bulletin 48, British Columbia Department of Mines and Petroleum Resources, Vancouver, British Columbia.

Holomuzi, J. 1995. Oviposition sites and fish-deterrent mechanisms in two steam anurans. 1995(3):607-613.

Hossack, B.R. and P.S. Corn. 2005. Changes in counts of Rocky Mountain Tailed Frog tadpoles after wildfire in Glacier National Park, Montana. Northwestern Naturalist 86(2):99-100. [abstract]

Hossack, B.R., and D.S. Pilliod. 2011. Amphibian responses to wildlife in the western United States: Emerging patterns from short-term studies. Fire Ecology 7(2):129-144.

Hossack, B.R., P.S. Corn, and D.B. Fagre. 2006. Divergent patterns of abundance and age-class structure of headwater stream tadpoles in burned and unburned watersheds. Canadian Journal of Zoology 84(10):1482–1488.

Hossack, B.R., M.J. Adams, E.H.C. Grant, C.A. Pearl, J.B. Bettaso, W.J. Barichivich, Winsor H. Lowe, K. True, J.L. Ware, and P.S. Corn. 2010. Low prevalence of chytrid fungus (*Batrachochytrium dendrobatidis*) in the amphibians of US headwater streams. Journal of Herpetology 44(2):253-260.

Howes, D.E., and E. Kenk. 1988. Terrain classification system for British Columbia (Revised edition). Recreational Fisheries Branch, Ministry of Environment, and Surveys and Resources Mapping Branch, Ministry of Crown Lands, Victoria, British Columbia. Ministry of Environment Manual 10.

Hudson, R.R., M. Slatkin, and W.P. Maddison. 1992. Estimation of levels of gene flow from DNA sequence data. Genetics 132(2):583-589.

Huggard, D.J. 2000. Developing animal-habitat models for management of high-elevation forests. PhD. Dissertation, Faculty of Forestry, University of British Columbia, Vancouver, British Columbia, Canada.

Hunter, M.G. 1998. Watershed-level patterns among stream amphibians in the Blue River Watershed, west-central Cascades of Oregon. MSc Thesis, Forest Sciences, Oregon State University, Corvallis, Oregon, USA. 97 p.

Hunter, M.A., T. Quinn, and M.P. Hayes. 2005. Low-flow spatial characteristics of forested headwater channels of southwest Washington. Journal of the American Water Resources Association 41(3):503–516.

IDFG [Idaho Department of Fish and Game]. 2006. Idaho Comprehensive Wildlife Conservation Strategy. Appendix B. Idaho Species of Greatest Conservation Need. Idaho Department of Fish and Game, Boise, Idaho. (http://fishandgame.idaho.gov/public/wildlife/cwcs/, accessed 13 November 2014)

IPCC [Intergovernmental Panel on Climate Change]. 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller (editors.)]. Cambridge University Press, Cambridge, United Kingdom and New York, New York, USA. 996 p.

Iredale, J.F. 2010. Presence not detected Coastal Tailed Frog inventory within the Cascades and Chilliwack Forest Districts. British Columbia Ministry of Environment, Kamloops, British Columbia, Canada. 26 p. (http://a100.gov.bc.ca/pub/siwe/details.do?id=4638, accessed on 7 October 2014)

Jackson, C.R., C.A. Sturm, and J.M. Ward. 2001. Timber harvest impacts on small headwater streams channels in the coast ranges of Washington. Journal of the American Water Resources Association 37(6):1533-1549.

Jackson, C.R., D.P. Batzer, S.S. Cross, S.M. Haggerty, and C.A. Sturm. 2007. Headwater streams and timber harvest: Channel, macroinvertebrate, and amphibian response and recovery. Forest Science 53(2):356-370.

Jaeger, R.G., and J.P. Hailman. 1973. Effects of intensity on the phototactic responses of adult anuran amphibians: a comparative survey. Zeitschrift für Tierpsychologie 33(3-4):352-407.

Jakob, M. 1999. The impacts of logging on landslide activity at Clayoquot Sound, British Columbia. Catena 38(4):1-22.

Jakober, M.J., T.E. McMahon, R.F. Thurow, and C.G. Clancy. 1998. Role of stream ice on fall and winter movements and habitat use by bull trout and cutthroat trout in Montana headwater streams. Transactions of the American Fisheries Society 127(2):223-235.

Jameson, D.L. 1955. Evolutionary trends in the courtship and mating behavior of Salientia. Systematic Zoology 4(3):105-119.

Jamieson, B., M. Lee, and K. Long. 1993. Ultrastructure of the spermatozoon of the internally fertilizing frog *Ascaphus truei* (Ascaphidae: Anura: Amphibia) with phylogenetic considerations. Herpetologica 49(1):52-65.

Jennings, M.R., and M.P. Hayes. 1994. Amphibian and reptile species of special concern in California. California Academy of Sciences and California Department of Fish and Game, Rancho Cordova, California, USA. 255 p.

Jones, J.A. and G.E. Grant. 1996. Peak flow responses to clear-cutting and roads in small and large basins, western Cascades Oregon. Water Resources Research 32(4):959-974.

Jones, J.A. and David A. Post. 2004. Seasonal and successional streamflow response to forest cutting and regrowth in the northwest and eastern United States. Water Resources Research 40:1-19.

Jones, J.L. 2008. A “tail” of two streams: Factors influencing Rocky Mountain tailed frog (*Ascaphus montanus*) tadpole distribution and abundance in Idaho and Montana. Master of Science Thesis, Department of Biological Sciences, Idaho State University, Pocatello, Idaho, USA. 104 p.

Jones, L.L.C. and M.G. Raphael. 1998. Natural history notes: *Ascaphus truei*. Predation. Herpetological Review, 29(1):39.

Jones, L.L.C., W.P. Leonard, and D.H. Olson (editors). 2005. Amphibians of the Pacific Northwest. Seattle Audubon Society, Seattle, Washington, USA. 227 p.

Jorgenson, E.E. 1997. Habitat suitability is a valuable concept. Wildlife Society Bulletin 25(3):602-603.

Jorgensen, C.B. 2000. Amphibian respiration and olfaction and their relationships: from Robert Townson (1794) to the present. Biological Reviews of the Cambridge Philosophical Society 75(3):297-345.

Karraker, N.E. 2001. *Ascaphus truei* (Tailed Frog). Predation. Herpetological Review 32(2):100.

Karraker, N.E. and G.S. Beyersdorf. 1997. A Tailed Frog (*Ascaphus truei*) nest site in northwestern California. Northwestern Naturalist 78(3):110-111.

Karraker, N.E, D.S. Pilliod, M.J. Adams, E.L. Bull, P.S. Corn, L.V. Diller, L.A. Dupuis, M.P. Hayes, B.R. Hossack, G.R. Hodgson, E.J. Hyde, K. Lohman, B.R. Norman, L.M. Ollivier, C.A. Pearl, and C.R. Peterson. 2006. Taxonomic variation in oviposition by Tailed Frogs (*Ascaphus*). Northwestern Naturalist 87(3):87-97.

Kasinsky, H.E., L. Gutovich, D. Kulak, M. Mackay, D.M. Green, J. Hunt, and J. Ausio. 1999. Protamine-like sperm nuclear basic proteins in the primitive frog *Ascaphus truei* and histone reversions among more advanced frogs. Journal of Experimental Zoology 284(7):717-728.

Kelsey, K.A. 1994. Reponses of headwater stream amphibians to forest practices in western Washington. Northwest Science 68(2):133.

Kelsey, K.A. 1995. Responses of headwater stream amphibians to forest practices in western Washington. PhD Dissertation, College of Forest Resources, Wildlife Sciences. University of Washington, Seattle, Washington. 167 p.

Kelsey, K.A. 2000. West-side stream amphibian surveys, Pp. 7-1 – 7-33. *In*: O’Connell, M.A., J.G. Hallett, S.D. West, K.A. Kelsey, D.A. Manuwal, and S.F. Pearson. 2000. Effectiveness of riparian management zones in providing habitat for wildlife. Timber Fish & Wildlife, Final Report TFW-LWAG1-00-001.

Kiffney, P.M., and J.S. Richardson. 2001. Interactions among nutrients, periphyton, and invertebrates and vertebrate (*Ascaphus truei*) grazers in experimental channels. Copeia 2001(2):422-429.

Kiffney, P.M., and J.P. Bull. 2001. Factors controlling periphyton accrual during summer in headwater streams of southwestern British Columbia, Canada. Journal of Freshwater Ecology 15(3):339-351.

Kiffney, P.M., J.S. Richardson, and J.P. Bull. 2003. Responses of periphyton and insect consumers to experimental manipulation of riparian buffer width along headwater streams in forested landscapes. Journal of Applied Ecology 40(6):1060-1076.

Kiffney, P.M., J.S. Richardson, and J.P. Bull. 2004. Establishing light as a causal mechanism structuring stream communities in response to experimental manipulation of riparian buffer width. Journal of the North American Benthological Society 23(3):542-555.

Kiffney, P.M., C.J. Volk, T.J. Beechie, G.L. Murray, G.R. Pess, and R.L. Edmonds. 2004. A high-severity disturbance event alters community and ecosystem properties in West Twin Creek, Olympic National Park, Washington, USA. Copeia 2004(2):422-429.

Kim, M.A. 1999. The influence of light and nutrients on interactions between a tadpole grazer and periphyton in two coastal streams. MSc Thesis, Department of Forest Sciences, University of British Columbia, Vancouver, British Columbia, Canada. 73 p.

Kroll, A.J. 2014. Personal communication to M. Hayes, 24 November.

Kroll, A.J., K. Risenhoover, T. McBride, E. Beach, B.J. Kernohan, J. Light, and J. Bach. 2008. Factors influencing stream occupancy and detection probability parameters of stream-associated amphibians in commercial forests of Oregon and Washington. Forest Ecology and Management 255(11):3726-3735.

Kroll, A.J. 2009. Sources of uncertainty in stream-associated amphibian ecology and responses to forest management in the Pacific Northwest, USA: a review. Forest Ecology and Management 257(4):1188-1199.

Kroll, A.J., J.G. MacCracken, T. McBride, J. Bakke, J. Light, P. Peterson, and J. Bach. 2010. Basin-scale surveys of stream-associated amphibians in intensively managed forests. Journal of Wildlife Management 74(7):1580-1587.

Kupferberg, S.J. 1997. The role of larval diet in anuran metamorphosis. American Zoologist 37(2):146.159.

Lamberti, G.A., and V.H. Resh. 1983. Stream periphyton and insect herbivores: An experimental study of grazing by a caddisfly population. Ecology 64(5):1124-1135.

Lamberti, G.A., S.V. Gregory, L.R. Ashkenas, R.C. Wildman, and K.M.S. Moore. 1991. Stream ecosystem recovery following a catastrophic debris flow. Canadian Journal of Fisheries and Aquatic Sciences 48(2):196-208.

Lamberti, G.A., S.V. Gregory, C.P. Hawkins, R.C. Wildman, L.R. Ashkenas, and D.M. DeNicola. 1992. Plant–herbivore interactions in streams near Mount St Helens. Freshwater Biology 27(2):237-247.

Lancaster, S.T., S.K. Hayes, and G.E. Grant. 2001. Modeling sediment and wood storage and dynamics in small mountainous watersheds, Pages 85– 102. *In*: J. M. Dorava (editor), Geomorphic Processes and Riverine Habitat, American Geophysical Union, Washington D.C., USA.

Landreth, H.F. and D.E. Ferguson 1967. Movements and orientation of the tailed frog, *Ascaphus truei*. Herpetologica 23(2):81-93.

Lapp, S., J. Byrne, I. Townshend, and S. Kienzle. 2005. Climate warming impacts on snowpack accumulation in an alpine watershed. International Journal of Climatology 25(4):521-536.

Laurila, A., B. Lindgren, and A.T. Laugen. 2008. Anti-predator defenses along a latitudinal gradient in *Rana temporaria*. Ecology 89:1399-1413.

Lawler J.J. and M. Mathias. 2007. Climate change and the future of biodiversity in Washington. Report prepared for the Washington Biodiversity Council. 42 p.

Lawler J.J., M. Mathias, A.E. Yahnke, and E.H. Girvetz. 2008. Oregon's biodiversity in a changing climate. Report prepared for the Climate Leadership Initiative, University of Oregon. 55 p.

Lee, Y.H. and A.S. Kwon. 1996. Ultrastructure of spermatozoa in Urodela and primitive Anura (Amphibia) with phylogenetic considerations. Korean Journal of Systematic Zoology 12:253-264.

Linsdale, J.M. 1933. Records of *Ascaphus truei* in Idaho. Copeia 1933(4):223.

Lohman, K. 2002. Annual variation in the density of stream tadpoles in a northern Idaho (USA) watershed. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 28:1-5.

Luce, C.H., and T.A. Black. 1999. Sediment production from forest roads in western Oregon. Water Resources Research 35(8):256-2570.

Luce, C.H., and T.A. Black. 2001. Spatial and Temporal Patterns in Erosion from Forest Roads, pp. 165-178. In: Wigmosta, M.S., and S.J. Burges (editor), Influence of Urban and Forest Land Uses on the Hydrologic-Geomorphic Responses of Watersheds. Water Resources Monographs, American Geophysical Union, Washington, D.C.

Lugo, A.E., and H. Gucinski. 2000. Function, effects, and management of forest roads. Forest Ecology and Management 133(3):249–262.

MacKenzie, D.I., J.D. Nichols, G.B. Lachman, S. Droege, and J.A. Royle. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83(8):2248-2255.

MacKenzie, D.I., J.D. Nichols, J.A. Royle, K.H. Pollock, L.L. Bailey, and J.E. Hines. 2006. Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence. Elsevier, San Diego, California, USA. 344 p.

Mallory, A. 2004. Coastal tailed frog (*Ascaphus truei*). *In* Accounts and measures for Managing Identified Wildlife – Accounts V. Victoria, British Columbia, Canada. 10 p.

Mallory, M.A., and J.S. Richardson. 2005. Complex interactions of light, nutrients and consumer density in a stream periphyton–grazer (tailed frog tadpoles) system. Journal of Animal Ecology 74(6):1020-1028.

Manlow, S.W. 1994. Geographic distribution. *Ascaphus truei*. Herpetological Review 25(1):31.

Manville, R.H. 1957. Amphibians and reptiles of Glacier National Park, Montana. Copeia 1957(4):308-309.

Marco, A., C. Quilchano, and A.R. Blaustein. 1999. Sensitivity to nitrate and nitrite in pond-breeding amphibians from the Pacific Northwest, USA. Environmental Toxicology and Chemistry 18(12):2836-2839.

Matthewes, R.W. 1985. Paleobotanical evidence for climate change in southern British Columbia during Late-glacial and Holocene time. Pp. 397-422. *In*: Harington, C.R. (editor), Climate Change in Canada 5: Critical Periods in the Quaternary Climatic History of Northern North America. Syllogeous, Number 55.

Matsuda, B.M. 2001. The effects of clear-cut timber harvest on the movement patterns of tailed frogs (*Ascaphus truei*) in southwestern British Columbia. MSc Thesis, Department of Forest Sciences, University of British Columbia, Vancouver, British Columbia, Canada. 103 p.

Matsuda, B.M., and J.R. Richardson. 2000. Clearcut timber harvest and movement patterns in tailed frogs. Pp. 485-488. *In*: Darling, L.M. (editor) Proceedings on the Biology and Management of Species and Habitats at Risk. Kamloops, British Columbia 15 - 19 Feb. 1999. Volume Two. British Columbia Ministry of Environment, Lands and Parks, Victoria, British Columbia and University College of the Cariboo, Kamloops, British Columbia, Canada. 520 p.

Matsuda, B.M., and J.R. Richardson. 2005. Movement patterns and relative abundance of coastal tailed frogs in clearcuts and mature forest stands. Canadian Journal of Forestry Research 35(5):1131-1138.

Matsuda, B.M., D.M. Green, and P.T. Gregory. 2006. Amphibians and reptiles of British Columbia. Royal BC Museum Handbook, Royal BC Museum, Victoria, Canada. 266 p.

Maughan, O.E. 1972. Distribution and geographic variation of sculpins in the Clearwater Basin. PhD dissertation, Washington State University, Department of Zoology, Pullman. 213 p.

Maughan, O.E., M.G. Wickham, P. Laumeyer, and R.L. Wallace. 1976. Records of the Pacific giant salamander, *Dicamptodon ensatus* (Amphibia, Urodela, Ambystomatidae) from the Rocky Mountains of Idaho. Journal of Herpetology 10(3):249-251.

Maughan, O.E., P. Laumeyer, R.L. Wallace and M.G. Wickham. 1980. Distribution of the tailed frog, *Ascaphus truei* Stejneger, in several drainages in northcentral Idaho. Herpetological Review 11(1):15-16.

Maxcy, K.A. 2000. The response of terrestrial salamanders to forest harvesting in southwestern British Columbia. MSc Thesis, Department of Forest Science, University of British Columbia, Vancouver, Canada. 91 p.

McComb, B.C., L. Curtis, C.L. Chambers, M. Newton, and K. Bentson. 2008. Acute toxic hazard evaluations of glyphosate herbicide on terrestrial vertebrates of the Oregon coast range. Environmental Science and Pollution Research 15(3):266–272.

Meentemeyer, V. and E.O. Box. 1987. Scale effects in landscape studies, Pp. 15-34. In: M.G. Turner (editor), Landscape heterogeneity and disturbance, Springer-Verlag, New York.

Meidinger, D. and J. Pojar. 1991. Ecosystems of British Columbia. Special Report Series 6. Ministry of Forests, Victoria, British Columbia, Canada. 330 p.

Metter, D.E. 1963. Stomach contents of Idaho larval *Dicamptodon*. Copeia 1963(2):435-436.

Metter, D.E. 1964*a*. A morphological and ecological comparison of two populations of the tailed frog, *Ascaphus truei* Stejneger. Copeia 1964(1):181-195.

Metter, D.E. 1964*b*. On breeding and sperm retention in *Ascaphus*. Copeia 1964(4):710-711.

Metter, D.E. 1966. Some temperature and salinity tolerances of *Ascaphus truei* Stejneger. Journal of the Idaho Academy of Science 4:44-47.

Metter, D.E. 1967. Variation in the ribbed frog *Ascaphus truei* Stejneger. Copeia 1967(3):634-649.

Metter, D.E. 1968. The influence of floods on population structure of *Ascaphus truei* Stejneger. Journal of Herpetology 1(1-4):105-106.

Metter, D.E., and R.J. Pauken. 1969. An analysis of the reduction in gene flow in *Ascaphus truei* in the northwest U.S. since the Pleistocene. Copeia 1969(2):301-307.

Millard, T. 1999. Debris flow initiation in coastal British Columbia gullies. Forest Research Technical Report 002 - Geomorphology. Vancouver Forest Region, Nanaimo, British Columbia, Canada.

Mittleman, M.B. and G.S. Myers. 1949. Geographical variation in the ribbed frog *Ascaphus truei*. Proceedings of the Biological Society of Washington 62(1):57-68.

MNHP [Montana Natural Heritage Program]. 2014. Montana Animal Species of Concern. Montana Natural Heritage Program, Helena, Montana. (http://mtnhp.org/SpeciesOfConcern/?AorP=a, accessed 13 November 2014).

Montgomery, D.R., and J.M. Buffington. 1997. Channel reach morphology in mountain drainage basins. Geological Society of America Bulletin 109(5):596-611.

Moore, M.K., and V.R. Townsend, Jr. 2003. Intraspecific variation in cranial ossification of the Tailed Frog, *Ascaphus truei*. Journal of Herpetology 37(4):714-717.

Moring, J.R., and R.L. Lantz. 1974. Immediate effects of logging on the freshwater environment of salmonids. Oregon Wildlife Commission Research Division Project, Final Report, AFS-58:1-101.

Moring, J.R., and R.L. Lantz. 1975. The Alsea watershed study: Effects of logging on the aquatic resources of three headwater streams of the Alsea River. Oregon Department of Fish and Wildlife, Fisheries Research Report 9:1-66.

Morrison, C. and J.-M. Hero. 2003. Geographic variation in life history characteristics of amphibians: A review. Journal of Animal Ecology 71(2):270-279.

Morrissey, C.A., and R.J. Olenick. 2004. American Dipper, *Cinclus mexicanus*, preys upon larval tailed frogs, *Ascaphus truei*. Canadian Field-Naturalist 118(3): 446-448.

Morrissey, C.A., L.L. Bendell-Young, and J.E. Elliott. 2004. Seasonal trends in population density, distribution, and movement of American Dippers within a watershed in southwestern British Columbia, Canada. Condor 106(4):815-825.

Mote, P.W. 2003a. Trends in temperature and precipitation in the Pacific Northwest during the twentieth century. Northwest Science 77(4):271–282.

Mote, P.W. 2003b. Trends in snow water equivalent in the Pacific Northwest and their climatic causes. Geophysical Research Letters 30(12)**,** 1601, doi:10.1029/2003GL017258.

Mote, P.W., E.A. Parson, A.F. Hamlet, W.S. Keeton, D.Lettenmaier, N. Mantua, E.L. Miles, D.W. Peterson, D.L. Peterson, R. Slaughter, A.K. Snover. 2003c. Preparing for climatic change: the water, salmon, and forests of the Pacific Northwest. Climatic Change 61(1-2):1-39.

Mote, P.W., A.F. Hamlet, M.P. Clark, and D.P. Lettenmaier. 2005. Declining mountain snowpack in western North America. Bulletin of the American Meteorological Society 86(1):39-49.

Müller, K. 1974. Stream drift as a chronobiological phenomenon in running water ecosystems. Annual Review of Ecology and Systematics 5:309-323.

Murphy, M.L. and J.D. Hall. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Canadian Journal of Fisheries and Aquatic Sciences 38(2):137-145.

Murphy, M.L., C.P. Hawkins, and N.H. Anderson. 1981. Effects of canopy modification and accumulated sediment on stream communities. Transactions of the American Fisheries Society 110(4):469-478.

Myers, G.S. 1931. *Ascaphus truei* in Humboldt County, California, with a note on the habits of the tadpole. Copeia 1931(2):56-57.

Myers, G.S. 1943. Notes on *Rhyacotriton olympicus* and *Ascaphus truei* in Humboldt County, California. Copeia 1943(2):125-126.

Nauman, R.S., and D.H. Olson. 2004. Surveys for terrestrial amphibians in Shasta County, California, with notes on the distribution of Shasta Salamanders (*Hydromantes shastae*). Northwestern Naturalist 85(1):35-38.

Newcombe, C.P. and D.D. MacDonald. 1991. Effects of suspended sediments on aquatic ecosystems. North American Journal of Fisheries Management 11(1):72-82.

Nielson, M., K. Lohman, and J. Sullivan. 2001. Phylogeography of the tailed frog *(Ascaphus truei*): Implications for the biogeography of the Pacific Northwest. Evolution 55(1):47-160.

Nielson, M., K. Lohman, C.H. Daugherty, F.W. Allendorf, K.L. Knudsen, and J. Sullivan. 2006. Allozyme and mitochondrial DNA variation in the Tailed Frog (Anura: *Ascaphus*): The influence of geography and gene flow. Herpetologica 62(3):235-258.

Nishikawa, K.C. and D.C. Cannatella. 1991. Kinematics of prey capture in the tailed frog *Ascaphus truei* (Anura: Ascaphidae). Zoological Journal of the Linnaean Society 103(3):289-307.

Nishikawa, K.C. and G. Roth. 1991. The mechanisms of tongue protraction during prey capture in the frog *Discoglossus pictus*. Journal of Experimental Biology 159:217-234.

Noble, G.K. 1925. An outline of the relation of ontogeny to phylogeny within the Amphibia. American Museum Novitates (165):1-17.

Noble, G.K. 1931. The biology of the Amphibia. First edition, McGraw-Hill Book Co., Inc., New York, New York, USA. 577 p.

Noble, G.K. and P.G. Putnam. 1931. Observations on the life history of *Ascaphus truei* Stejneger. Copeia 1931(3):97-101.

Nussbaum, R.A., E.D. Brodie Jr., and R.M. Storm. 1983. Amphibians and Reptiles of the Pacific Northwest. University of Idaho Press, Moscow, Idaho, USA. 332 p.

O'Connell, M.A., J.G. Hallett, S.D. West, K.A. Kelsey, D.A. Manuwal, and S.F. Pearson. 2000. Effectiveness of riparian management zones in providing habitat for wildlife. Timber Fish & Wildlife, Final Report TFW-LWAG1-00-001. Various pagination.

Oliver, C.D., and B.C. Larson. 1996. Forest Stand Dynamics. John Wiley and Sons, New York, New York, USA. 544 p.

Olson, D.H. 2012. Personal communication to M. Hayes, 17 May.

Olson, D.H., and Rugger. 2007. Preliminary study of the effects of headwater riparian reserves with upslope thinning on stream habitats and amphibians in western Oregon. Forest Science 53(2):331-342.

Olson, D.H., and G. Weaver. 2007. Vertebrate assemblages associated with headwater hydrology in western Oregon managed forests. Forest Science 53(2):343-355.

OBIC [Oregon Biodiversity Information Center]. 2013. Rare, Threatened and Endangered Species of Oregon. Oregon Natural Heritage Information Center, Portland State University, Portland, Oregon, USA. 111 p. [July] (http://orbic.pdx.edu/, accessed 13 November 2014)

Palmeri-Miles, A.F., K.A. Douville, J.A. Tyson, K.D. Ramsdell, and M.P. Hayes. 2010. Field observations of oviposition and early development of the Coastal Tailed Frog (*Ascaphus truei*). Northwestern Naturalist 91:206-213.

Paige, K. 2014. Personal communication to Marc Hayes, 8 October 2014.

Palmquist, R. 2005. Type N stream demarcation study: Phase I: Pilot results. Final Report, Washington State Cooperative Monitoring, Evaluation, and Research Committee, Olympia, Washington. 61 p.

Pauken, R.J., and D.E. Metter. 1971. Geographic representation of morphologic variation among populations of *Ascaphus truei* Stejneger. Systematic Zoology 20(4):434-441.

Peterson, N.P. 2011. Personal communication to M. Hayes, 9 May.

Pfankuch, D.J., 1975. Stream reach inventory and channel stability evaluation. USDA Forest Service, R1-75-002. Government Printing Office #696-260/200, Washington DC, 26 pp.

Pilliod, D.S., R.B. Bury, E.J. Hyde, C.A. Pearl and P.S. Corn. 2003. Fire and amphibians in North America. Forest Ecology and Management 178(1-2):163-181.

Pilliod, D.S., P.S. Corn, R.B. Bury, and E.J. Hyde. 2004. Effects of wildland fires on stream amphibian populations in the greater Northwest. Northwestern Naturalist 85:85-86. [abstract]

Pilliod, D.S., T.B. Jain, J.S. Evans, R.B. Bury, and P.S. Corn. 2005. The effects of burn severity on stream amphibian populations. Northwestern Naturalist 86(2):113-114.

Pollett, K.L., J.G. MacCracken, and J.A. MacMahon. 2010. Stream buffers ameliorate the effects of timber harvest on amphibians in the Cascade Range of southern Washington, USA. Forest Ecology and Management 260(6):1083-1087.

Quinn, T., M.P. Hayes, D.J. Dugger, T.L. Hicks, and A. Hoffman. 2007. Comparison of two techniques for surveying headwater stream amphibians. Journal of Wildlife Management 71(1):282-288.

Railsback, S.F., H.B. Stauffer, and B.C. Harvey. 2003. What can habitat preference models tell us? Tests using a virtual trout population. Ecological Applications 13(6):1580-1594.

Reeves, G.H., P.A. Bisson, and J.M. Dambacher. 1998. Fish Communities. Pages 200-254. In: Naiman, R.J., and R.E. Bilby (editors), River Ecology and Management: Lessons from the Pacific Coastal Ecoregion, Springer-Verlag, New York, New York, USA.

Regonda, S.K., B. Rajagopalan, M. Clark, and J. Pitlick. 2005. Seasonal cycle shifts in hydroclimatology over the western United States. Journal of Climate 18(2)**:**372–384.

Reid, L.M., and T. Dunne. 1984. Sediment production from forest road surfaces. Water Resources Research 20(11):1753-1761.

Reiss, J.O. and H.L. Eisthen. 2008. Comparative anatomy and physiology of chemical senses in amphibians, Pp. 43-63. *In*: J.G.M. Thewissen and S. Nummela (editors), Sensory Evolution on the Threshold: Adaptations in Secondarily Aquatic Vertebrates, University of California Press, Berkeley, California, USA.

Rhee, H., J.L. Fridely, and R.B. Foltz. 2004. Modeling erosion from unpaved forest roads at various levels of geometric detail using WEPP model. Trans. ASAE 47(3):961–968.

Rice, R.M., F.B. Tilley, and P.A. Datzman. 1979. A watershed's response to logging and roads: South Fork of Caspar Creek, 1967-76. US Department of Agriculture, Pacific Southwest Forest and Range Experiment Station, Forest Service., Berkeley, California, Research Paper PSW-146:1-12. [illustrated].

Richardson, J.S. 2014. Personal communication to M. Hayes, 3 March.

Richardson, J.S. and W.E. Neill. 1995. Distribution patterns of two montane stream amphibians and the effects of forest harvest: the Pacific giant salamander and tailed frog in southwestern British Columbia. Habitat Conservation Fund, Resource Inventory Committee, Skagit Environmental Endowment Commission, and British Columbia Ministry of Environment, Lands and Parks. Victoria, British Columbia, Canada.

Richardson, J.S. and W.E. Neill. 1998. Headwater amphibians and forestry in British Columbia: Pacific giant salamanders and tailed frogs. Northwest Science 72 (Special Issue 2):122-123.

Ricker, W.E. and E.B.S. Logier. 1935. Notes on the occurrence of the ribbed toad (*Ascaphus truei,* Stejneger) in Canada. Copeia 1935(1):46.

Ritland, K., L.A. Dupuis, F.L. Bunnell, W.L.Y. Hung, and J.E. Carlson. 2000. Phylogeography of the tailed frog (*Ascaphus truei*) in British Columbia. Canadian Journal of Zoology 78(10):1749-1758.

Rodgers, T.L. and W.L. Jellison. 1942. A collection of amphibians and reptiles from western Montana. Copeia 1942(1):10-13.

Rollerson, T.P., B. Thomson, and T. Millard. 1997. Identification of coastal British Columbia terrain susceptible to debris flows. In "Debris-flow hazards mitigation: mechanics, prediction and assessments". First International Conference of the American Society of Civil Engineers, August 7-9, 1997, San Francisco, California.

Roni, P. 2002. Habitat use by fishes and Pacific giant salamanders in small western Oregon and Washington streams. Transactions of the American Fisheries Society 131(4):743-761.

Roni, P. 2003. Responses of benthic fishes and giant salamanders to placement of large woody debris in small Pacific Northwest streams. North American Journal of Fisheries Management 23(4):1087-1097.

Round, F.E., and Crawford, R.M. 1990. *The Diatoms: Biology and Morphology of the Genera*. Cambridge University Press, United Kingdom. 760 pp.

Rosenberger, A.E., and J.E. Dunham. 2005. Validation of abundance estimates from mark-recapture and removal techniques for rainbow trout captured by electrofishing in small streams. North American Journal of Fisheries Management 25:1395-1410.

Russell, A.P., and A.M. Bauer 2001. Amphibians and reptiles of Alberta: A field guide and primer of boreal herpetology. University of Calgary Press, Calgary, Alberta, Canada. 279 p.

Salt, G.W. 1952. The belltoad, *Ascaphus truei*, in Mendocino County, California. Copeia 1952(3):193-194.

Sauder, E.A., R.K. Krag, and G.V. Wellburn. 1987. Logging and mass wasting in the Pacific Northwest with Application to the Queen Charlotte Islands, British Columbia: A literature review. Forest Engineering Research Institute of Canada (FERIC) Special Report No. SR-45. British Columbia Ministry of Forests and British Columbia Ministry of Environment, Lands, and Parks, Victoria, British Columbia, Canada.

Sawyer, J.O., S.C. Sillett, J.H. Popenoe, A. LaBanca, T. Sholars, D.L. Largent, F. Euphrat, R.F. Noss, and R. Van Pelt, 2000. Characteristics of redwood forests, Pp. 39–79. *In*: Noss, R.F. (editor), The Redwood Forest: History, Ecology, and Conservation of the Coast Redwoods. Island Press, Covelo, CA, USA,

Schonberger, C.F. 1945. Food of some amphibians and reptiles of Oregon and Washington. Copeia 1945(2):120-121.

Sepulveda, A.J., and W.H. Lowe. 2009. Local and landscape influences on the occurrence and density of *Dicamptodon aterrimus*, Idaho Giant Salamander. Journal of Herpetology 43(3):469-484.

Sever, D.M., E.C. Moriarty, L.C. Rania, and W.C. Hamlett. 2001. Sperm storage in the oviduct of the internal fertilizing frog *Ascaphus truei*. Journal of Morphology 248(1):1-21.

Shaffer, H.B., G.M. Fellers, S.R. Voss, J.C. Oliver, and G.B. Pauly. 2004. Species boundaries, phylogeography and conservation genetics of the red-legged frog (*Rana aurora/draytonii*) complex. Molecular Ecology 13(10):3033-3039.

Shapovalov, L. 1937. Third record of *Ascaphus truei* in California. Copeia 1937(4):234.

Simons, L.H. and M. Simons 1998. Geographic distribution. *Ascaphus truei*. Herpetological Review 29(2):106.

Slater, J.R. 1931. Mating behavior of *Ascaphus truei* Stejneger. Copeia 1931(2):62-63.

Slater, J.R. 1955. Distribution of Washington Amphibians. Occasional Papers, Department of Biology, College of Puget Sound (16):120-154.

Slipp, J.W., and G.C. Carl. 1943. Northward extensions of the range of *Ascaphus*. Copeia 1943(2):127.

Smith, E.P. 2002. BACI design, Pp. 141-148. *In*: A.H. El-Shaarawi and W.W. Piegorsch (editors), Encyclopedia of Environmetrics, John Wiley & Sons, Ltd, Chichester, New York.

Smith, H.M. 1932. *Ascaphus truei* Stejneger in Montana. Copeia 1932(2):100.

Smith, S.N. 1997. Geographic distribution. *Ascaphus truei*. Herpetological Review 28(1):47.

Spear, S.F., and A. Storfer 2008. Landscape genetic structure of coastal tailed frogs (*Ascaphus truei*) in protected vs. managed forests. Molecular Ecology 17:4642-4656.

Spear, S.F., and A. Storfer. 2010. Anthropogenic and natural disturbance lead to differing patterns of gene flow in the Rocky Mountain tailed frog (*Ascaphus montanus*). Biological Conservation 143:778-786.

Spear, S.F., C.M. Crisafulli, and A. Storfer. 2012. Genetic structure among coastal tailed frog populations at Mount St. Helens is moderated by post-disturbance management. Ecological Applications 22(3):856-869.

Spies, T.A., and J.F. Franklin. 1991. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington. Pages 91-109. *In*: Ruggiero, L.F., K.B. Aubry, A.B. Carey and M.H. Huff (editors), Wildlife and Vegetation of Unmanaged Douglas-fir Forests. USFS Pacific Northwest Research Station. PNW-GTR-285, Olympia, Washington, USA.

Spies, T.A., J.F. Franklin, and T.B. Thomas. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology 69(6):1689-1702.

Spromberg, J.A., and W.J. Birge. 2005. Population survivorship index for fish and amphibians: Application to criterion development and risk assessment. Environmental Toxicology and Chemistry 24(6):1541-1547.

Stebbins, R.C. 1985. A field guide to western reptiles and amphibians. 2nd edition, Peterson Field Guide Series. Houghton Mifflin Co., Boston, Massachusetts, USA. 336 p.

Stebbins, R.C. 1951. Amphibians of western North America. University of California Press, Berkeley, California, USA. 539 p.

Stebbins, R.C. 2003. A field guide to western reptiles and amphibians. 3rd edition, Peterson Field Guide Series. Houghton Mifflin Co., Boston, Massachusetts, USA. 533 p.

Stejneger, L.H. 1899. Description of a new genus and species of discoglossoid toad from North America. Proceedings of the United State National Museum 21(1178):899-901.

Stephenson, B. and P. Verrell. 2003. Courtship and mating of the tailed frog (*Ascaphus truei*). Journal of Zoology (London) 259(1):15-22.

Stewart, I.T., D.R. Cayan, and M.D. Dettinger. 2004. Changes in snowmelt runoff timing in western North America under a 'business as usual' climate change scenario. Climatic Change 62(1-3):217-232.

Stewart, I.T., D.R. Cayan, and M.D. Dettinger. 2005. Changes toward earlier streamflow timing across western North America. Journal of Climate 18(8):1136-1155.

Stoddard, M.A., and J.P. Hayes. 2005. The influence of forest management on headwater stream amphibians at multiple spatial scales. Ecological Applications 15(3):811– 823.

Strahler, A.N. 1952. Hypsometric (area-altitude) analysis of erosional topography. Bulletin of the Geological Society of America 63(11):1117-1142.

Sutherland, G.D. 2000. Risk assessment for conservation under ecological uncertainty: a case study using a stream-dwelling amphibian in managed forests. Ph.D. Dissertation, Department of Forest Sciences, University of British Columbia, Vancouver, British Columbia, Canada. 164 p.

Sutherland, G.D., J. S. Richardson, and F.L. Bunnell. 2001. Uncertainties linking tailed frog habitat and population dynamics with riparian management. Pp. 477-483 *In*: L. M. Darling (editor). 2000. Proceedings of a Conference on the Biology and Management of Species and Habitats at Risk, Kamloops, B.C., 15 - 19 Feb., 1999. Volume Two. B.C. Ministry of Environment, Lands and Parks, Victoria, British Columbia, and University College of the Cariboo, Kamloops, British Columbia, Canada.

Sutherland, G.D. and F.L. Bunnell. 2001. Cross-scale classification trees for assessing risks of forest practices to headwater stream amphibians. Pp. 550-555 *In*: Johnson, D.H. and T.A. O'Neil (managing directors), Wildlife-Habitat Relationships in Oregon and Washington. Oregon State University Press, Corvallis, Oregon.

Svihla, A. 1933. Extension of the ranges of some Washington Amphibia. Copeia 1933(1):39.

Svihla, A. and R.D. Svihla 1933. Notes on *Ascaphus truei* in Kittitas County, Washington. Copeia 1933(1):37-38.

Svihla, A. 1959. A simple method of collecting *Ascaphus truei* tadpoles. Copeia 1959(1):72.

Swanson, F.J., S.L. Johnson, S.V. Gregory, and S.A. Acker. 1998. Flood disturbance in a forested mountain landscape: Interaction of land use and floods. BioScience 48(9):681-689.

Turner, F.B. 1962. The demography of frogs and toads. Quarterly Review of Biology 37(4):303-314.

Van Denburgh, J. 1912. Notes on *Ascaphus*, the discoglossid toad of North America. Proceedings of the California Academy of Sciences, Fourth Series 3:259-264.

Van Winkle, K. 1922. Extension of the range of *Ascaphus truei* Stejneger. Copeia (102):4-6.

Visalli, D. and W.P. Leonard W.P. 1994. Geographic distribution. *Ascaphus truei*. Herpetological Review 25(1):31.

Vonesh, J.R., and O. de la Cruz. 2002. Complex life cycles and density dependence: assessing the contribution of egg mortality to amphibian declines. Oecologia 133:325-333.

Vredenburg, V.T. 2004. Reversing introduced species effects: Experimental removal of introduced fish leads to rapid recovery of a declining frog. Proceedings of the National Academy of Sciences 101(2):7646-7650.

Wahbe, T.R. 1996. Tailed frogs (*Ascaphus truei*, Stejneger) in natural and managed coastal temperate rainforests of southwestern British Columbia, Canada. Centre for Applied Conservation Biology. MSc Thesis, Department of Forest Sciences, The University of British Columbia, Vancouver, British Columbia, Canada. 49 p.

Wahbe, T.R. 2000. Preliminary Species Habitat Model for the Tailed Frog (*Ascaphus truei*). British Columbia Conservation Foundation and Centre for Applied Conservation Biology. Unpublished Report. Keystone Wildlife Research. White Rock, British Columbia, Canada. 14 p.

Wahbe, T.R. and F.L. Bunnell. 2000. Defining Habitat Conservation Areas for Tailed Frogs. University of British Columbia. Centre for Applied Conservation Biology. Progress Report to Wildlife Habitat Canada. Ottawa, Ontario, Canada. 24 p.

Wahbe, T.R. and F.L. Bunnell. 2001. Preliminary observations on movements of tailed frog tadpoles (*Ascaphus truei*) in streams through harvested and natural Forests. Northwest Science 75(1):77-83.

Wahbe, T.R., and F.L. Bunnell. 2003. Relations among larval tailed frogs, forest harvesting, stream microhabitat, and site parameters in southwestern British Columbia. Canadian Journal of Forest Research 33(7):1256–1266.

Wahbe, T.R., F.L. Bunnell, and R.B. Bury. 2000. Defining Wildlife Habitat Areas for Tailed Frogs. Pp. 489-495. *In*: Darling, L.M. (editor) Proceedings on the Biology and Management of Species and Habitats at Risk. Kamloops, British Columbia 15 - 19 Feb. 1999. Volume Two. British Columbia Ministry of Environment, Lands and Parks, Victoria, British Columbia and University College of the Cariboo, Kamloops, British Columbia, Canada.

Wahbe, T.R., F.L. Bunnell, and R.B. Bury. 2004. Terrestrial movements of juvenile and adult tailed frogs in relation to timber harvest in coastal British Columbia. Canadian Journal of Forest Research 34(12):2455-2466.

Wahbe, T.R., C. Ritland, F.L. Bunnell, and K. Ritland. 2005. Population genetic structure of tailed frogs (*Ascaphus truei*) in clearcut and old-growth stream habitats in south coastal British Columbia. Canadian Journal of Zoology 83(11):1460-1468.

Wallace, R.L. and L.V. Diller. 1998. Length of larval cycle of *Ascaphus truei* in coastal streams of the Redwood Region, northern California. Journal of Herpetology 32(3):404-409.

WDFW [Washington Department of Fish and Wildlife]. 2014. Washington State Species of Concern Lists. (http://wdfw.wa.gov/conservation/endangered/lists/; accessed on 13 November 2014)

Wassersug, R.J., and D.G. Sperry. 1977. The relationship of locomotion to differential predation on *Pseudacris triseriata*. Ecology 58(4):830-839.

Waterstrat, T.F., R.L. Crawford, and M.P. Hayes. 2007. *Ascaphus truei* (Tailed Frog). Spider Prey. Herpetological Review 38(3):318.

WDNR [Washington Department of Natural Resource]. 2009. Forest Practices Habitat Conservation Plan. (http://www.dnr.wa.gov/BusinessPermits/Topics/ForestPracticesHCP/Pages/fp_hcp.aspx)

Weaver, G. 2012. Personal communication to M. Hayes, 19 May.

Weir, B.S. and C.C. Cockerham. 1984. Estimating *F*-statistics for the analysis of population structure. Evolution 38(6):1358–1370.

Welsh, H.H., Jr. 1985. Geographic distribution. *Ascaphus truei*. Herpetological Review 16(2):59.

Welsh, H.H., Jr. 1990. Relictual amphibians and old-growth forests. Conservation Biology 4(3):309-319.

Welsh, H.H., Jr. 1993. A hierarchical analysis of the niche relationships of four amphibians from forested habitats of northwestern California. PhD Dissertation, University of California, Berkeley, California, USA. 202 p.

Welsh, H.H., Jr. 2011. Frogs, fish and forestry: An integrated watershed network paradigm conserves biodiversity and ecological services. Diversity 3:503-530.

Welsh, H.H., Jr. 2014. Personal communication to M. Hayes, 15 December 2011.

Welsh, H.H., Jr. and A.J. Lind. 1991. The structure of the herpetofaunal assemblage in the Douglas-fir/hardwood forests of northwestern California and southwestern Oregon. Pp. 395-413. *In*: Aubry, K.B., A.B. Carey and M.H. Huff (editors), Wildlife and Vegetation of Unmanaged Douglas-fir Forests. USFS Pacific Northwest Research Station. PNW-GTR-285, Olympia, Washington, USA.

Welsh, H.H., Jr., and A.J. Lind. 2002. Multiscale habitat relationships of stream amphibians in the Klamath-Siskiyou region. Journal of Wildlife Management 66(3):581-602.

Welsh, H.H., Jr. and L.M. Ollivier. 1998. Stream amphibians as indicators of ecosystem stress: A case study from California's redwoods. Ecological Applications 8(4):1118-1132.

Welsh, H.H., Jr. and R.J. Reynolds. 1986. *Ascaphus truei* (tailed frog). Herpetological Review 17(1):19.

Welsh, H.H., Jr., L.M. Ollivier, and D.R. Hankin. 1997. A habitat-based design for sampling and monitoring stream amphibians with an illustration from Redwood National Park. Northwestern Naturalist 78(1):1-16.

Werner, J.K., B.A. Maxell, P. Hendricks, D.L. Flath. 2004. Amphibians and reptiles of Montana. Mountain Press Publishing Company, Missoula, Montana, USA. 262 p.

Wernz, J.G. 1969. Spring mating of *Ascaphus*. Journal of Herpetology 3(3-4):167-169.

Wernz, J.G., and R.M. Storm. 1969. Pre-hatching stages of the tailed frog, *Ascaphus truei* Stejneger. Herpetologica 25(2):86-93.

WFPB (Washington Forest Practices Board). 2001. Washington Forest Practices. Washington Department of Natural Resources, Olympia, Washington. varied pagination [July]

Wikipedia. 2014. Tailed frog. Answers.com (http://www.answers.com/topic/tailed frog, accessed 7 October 2014).

Wilkins, R.N. 2011. Personal communication to M. Hayes, 8 May.

Wilkins, R.N. and N.P. Peterson. 2000. Factors related to amphibian occurrence and abundance in headwater streams draining second-growth Douglas-fir forests in southwestern Washington. Forest Ecology and Management 139(1):79-91.

Wind, E. 2009. Coastal tailed frog inventory and habitat assessment: BCRP project number: 09.W.BRG.01. Final Report, E. Wind Consulting, Nanaimo, British Columbia, Canada.

Wood, W.F. 1939. Amphibian records from northwestern California. Copeia 1939(2):110.

Wright, K.A., K.H. Sendek, R.M. Rice, and R.B. Thomas. 1990. Logging effects on streamflow: Storm runoff at Caspar Creek in northwestern California. Water Resources Research 26(7):1657-1667.

Zweifel, R.G. 1955. Ecology, distribution, and systematics of frogs of the *Rana boylei* group. University of California Publications in Zoology 54(4):207-292.

APPENDIX I

In the version of this document developed prior to the partitioning of tailed frogs into two species, one of the authors (Sutherland) had developed a basic demographic model to allow preliminary perspective on tailed frog population dynamics. That model had been developed from a blend of information from the two species now recognized. Significant life history differences emerging between the species (see LIFE HISTORY section) will require model revision. Nonetheless, to preserve the original intent of this effort, we provide the basis of information obtained for this model as well as equivalent more recently collected data that should be useful in future work.

Using composite data from the two tailed frog species now recognized, Sutherland (2000), modeled the average population growth rate (lambda: λ), estimating that it was close to 1.0 over the range of variation in demographic parameters. He also deduced that even incorporating the most optimistic assumptions, λ would rarely exceeded 1.2. Other work on vertebrates suggests that similar values of λ characterize long-lived taxa (Heppell 1998). Actual longevity of both tailed frog species is unclear, but for a frog, fair longevity is suspected. The work of Daugherty and Sheldon (1982b) indicates that 7-8 years seem to be required to reach reproductive maturity in *A. montanus,* based on evidence that the pre-metamorphic interval appears to 3 years in populations examined to date (see LIFE HISTORY section), and that Daugherty and Sheldon (1982b) determine that 4-5 years post-metamorphosis were needed to achieve reproductive maturity, variation at least partly dependent on gender (on average males mature a year earlier than females). Daugherty and Sheldon (1982b) also estimated that the oldest verifiable age of 543 mark-recaptured frogs they had was 14 years, but assignment of individuals to ages 9 or older had to be done exclusively from multi-year recaptures, of which few existed. Hence, population-level average and maximum longevity or how longevity varies among *A. montanus* populations is not known. Burkholder and Diller (2007) found that 2-3 years post-metamorphosis are needed to reach sexual maturity in *A. truei*, but no estimates of *A. truei* adult longevity exist.

Appendix Table 1 compares the duration of *Ascaphus* life stages that Sutherland (2000) used to structure his survivorship estimates to available data now partitioned across the two species by the life stages he originally used. It should be recognized that his large and small tadpole stages are an arbitrary partitioning of tailed frog development since size was the only criterion distinguishing those stages. Lability of size to diverse factors makes it difficult to meaningfully compare these categories to other datasets. Estimates are also lacking for the duration of metamorphosis for either species, a brief interval (likely less than one month) that Sutherland (2000) modeled as part of his juvenile life stage. Juveniles are also the only stage for which Sutherland (2000) likely misestimated duration; Daugherty and Sheldon (1982b) found that *A. montanus* spends 4-5 years as juveniles, whereas Burkholder and Diller (2007) reported 2-3 years for *A. truei* near the southern end of its range, so the value for British Columbia, at northern end of the range of both species, is likely greater than the 1-2 years proposed by Sutherland.

Reliable estimates of survivorship (from mark-recapture data or cohort analysis) of the different *Ascaphus* life stages are scarce for either species. Sutherland (2000) combined theoretical expectations with data estimates from southern British Columbia to derive his estimates. Two theoretical expectations derived from data on amphibian populations in general were underpinnings: 1) survivorship of eggs and larvae is low (relative to other life stages), and 2) mortality of juveniles fluctuates to a greater degree than that of adults (Duellman and Trueb 1994). By examining larval size-frequency data for sites in southern British Columbia, Sutherland (2000) estimated annual survivorship for larvae in British Columbia to be between 0.25 and 0.50 with annual variation of up to 40%. Sutherland (2000) further reasoned that in most streams, eggs/hatchlings and tadpoles likely share many of the same sources of mortality, so he approximated the unknown annual eggs/hatchling survival rate using the midpoint of the range of larval survival (0.375). These estimates of larval survival may be correct for British Columbia, but we would expect them to progressively overestimate survivorship as one moves south if the latitudinal trend in increased stream production with southerly latitude supports more predators (Laurila *et al.* 2008). Further, both empirical data and modeling have suggested that survivorship of eggs among temperate amphibian is higher than that of the larval stages (Vonesh and de la Cruz 2002, Gunzburger and Travis 2005), so at least the egg portion of egg/hatchling survivorship may be higher than the Sutherland (2000) estimates. Based on the second general premise, Sutherland (2000) estimated survival of metamorphosed juveniles to be slightly lower than adults because of their mortality risks are potentially greater than adults from disturbances (e.g., severe freshets), predators, and dispersal (see LIFE HISTORY section).

APPENDIX TABLE 1. Comparison of estimates of the duration of various *Ascaphus* life stages from Sutherland (2000) to available data. Current sources are color coded by the species for which data exist; red for *Ascaphus montanus* and blue for *A. truei*. Bi-colored sources provide data for both species with the more substantial data for the species with the first color. UNK indicates that the duration of the life stage is unknown.

Life Stage	Duration of Life Stage				
	Sutherland (2000)	Sutherland Source	*Ascaphus montanus*	*Ascaphus truei*	Current Source
Eggs	<1 year	Duellman and Trueb (1994)	23 days	21 days	Karraker *et al.* (2006)
Hatchlings			3 years	1-4 years	Metter (1964) Metter (1967) Brown (1990) Bull and Carter (1996a) Wallace and Diller (1998) Bury and Adams (1999)
Small tadpoles	1-2 years	Sutherland (2000)			
Large tadpoles	1-2 years	Sutherland (2000)			
Metamorphs	1-2 years	—	UNK	UNK	—
Juveniles			3-4 years	2-3 years	Daugherty and Sheldon (1982b) Burkholder and Diller (2007)
Adults	7+ years	Daugherty and Sheldon (1982b)	7+ years	UNK	Daugherty and Sheldon (1982b)

APPENDIX TABLE 2. Estimates of annual survivorship for various *Ascaphus* life stages from Sutherland (2000). Quality of Data was a tool that Sutherland (2000) provided to score the quality of empirical data underlying survivorship estimates on a 1-5 scale as 1 (high uncertainty) up to 5 (certain knowledge). Major sources of mortality for each stage are listed in likely descending order of importance.

Life Stage	Annual Survivorship			
	Survivorship estimates (per capita rate/year)	Sutherland Source	Quality of Data	Major Sources of Mortality
Eggs/ Hatchlings	0.38	Duellman and Trueb (1994)	4	predation erosion disturbance
Small tadpoles	0.25-0.5	Sutherland (2000)	3	predation aperiodic floods debris flows high temperatures desiccation
Large tadpoles	0.25-0.5	Sutherland (2000)	3	predation aperiodic floods
Metamorphs	0.7	—	1	predation desiccation floods
Juveniles				
Adults	0.8	Daugherty & Sheldon (1982b)	3	predation senescence desiccation

Since Sutherland (2000) developed estimates for his pre-species split model, species-specific estimates of annual survivorship by life stage have been calculated for *A. truei* (N. Chelgren, pers. comm.), but these are not yet published. Estimates for juveniles and adults from Sutherland's model are entirely for *A. montanus*, as these were drawn from Daugherty and Sheldon (1982b). However, uncertainty about the duration of the juvenile interval (see earlier discussion) may require re-determination of the annual survivorship estimates made from Daugherty and Sheldon (1982b). Further, given their substantive recapture data, annual survivorship could be estimated for juvenile and adult *A. truei* from the data of Burkholder and Diller (2007), and for larvae potentially from the size-frequency distributions of *A. truei* larvae reported by Wallace and Diller (1998).

Further, the major sources of mortality that Sutherland (2000) suggested as impinging on various life stages will require re-consideration. In particular, debris flows, which dominate major channel organization processes in headwater streams (Brummer and Montgomery 2003), can affect all life stages that are near enough to the stream to be in the path of the debris flow, but in general, debris flows are infrequent on short (multi-decadal) time scales. However, they may be less frequent under most climate change scenarios predicted for the Pacific Northwest, which reveal more precipitation in general, more of that precipitation as rain, and an increased frequency of extreme precipitation events (see CLIMATE CHANGE section). Further, it is unclear how accessible to predators the eggs or hatchlings of tailed frogs really are, especially to predators large enough to consume them, since both are well concealed in the interstices of stream substrates. How much of a mortality problem higher water temperatures really are for eggs, hatchlings and small larvae is also unclear because ground, surface and precipitation inputs to streams are complex and have varied temperature signatures. However, higher water temperatures may be more of a problem for *A. truei* than for *A. montanus*, especially when climate change really begins to affect stream water temperatures. Lastly, adult and juvenile tailed frogs can effectively avoid desiccation by moving into hydric refuges unless drought is so extreme that such refuges are largely eliminated on a region-wide large scale, so outside of extreme conditions, desiccation may not be an important source of mortality to post-metamorphic life stages.

POPULATION DATA

The original version of this document also contained a section discussing population data. Evaluating trends and their causes in *Ascaphus* populations is difficult enough when one incorporates detectability into population estimates, which to date no study has done though two near-complete major studies have such estimates (see the POTENTIAL EFFECTS OF FORESTRY PRACTICES section). As a consequence, available data from studies to date is impossible to effectively interpret. However, we provide them here with their respective modes of collection so that at some future time, cross-comparisons may be made if and when understanding of variation in detectability with type of sampling can be integrated with detectability as a consequence of diverse other factors (season, water temperature, various aspects of habitat complexity and so forth). The basic problem is that these diverse other factors co-contribute to variability in *Ascaphus* abundance, and because detectability is factor-specific, its respective contribution to variability for any particular factor set is largely unknown. This creates uncertainty of unknown dimensions, making estimating abundance impossible. Hence, here, we present density data uncorrected for detectability with the understanding that it is biased by unclear uncertainties.

Densities of larval *A. truei* have been measured as ranging from as low as 0.09 larvae/m^2 in unmanaged old-growth on the Olympic Peninsula to as high as 9.7 larvae/m^2 measured in timber-managed landscape in central coastal British Columbia (Appendix Table 3).

The total population size of *A. truei* is currently unknown (Dupuis *et al*. 2000) and cannot easily be estimated based on existing data. The juvenile and adult life stages of *Ascaphus* are difficult to census, and most data on densities and abundances of *Ascaphus* are based on larval surveys. Hawkins and Crisafulli (*unpubl. data*) attempted to estimate the adult *A. truei* population size in a small watershed (size not specified) of predominantly old-growth forest near Mount St. Helens. Using an estimate of 38,176 larvae, if female frogs produce 55 eggs each year (clutch size was a mean for Mt. St. Helens area, but see LIFE HISTORY section), the numbers of females needed to produce the estimated number of larvae in the watershed was 694. If females reproduce every two years, these estimates would have to be doubled. If the sex ratio is assumed to be 1:1, the minimum number of adult *A. truei* in these basins would be 1,388 to 2,776. Sutherland (2000) attempted to use available population and demographic data to estimate population sizes in streams of varying habitat characteristics using population models. He concluded that three key uncertainties prevent adequate estimates of *Ascaphus* population sizes: 1) fundamental demographic characteristics of *Ascaphus* (especially survival rates), 2) area and carrying capacity of aquatic and adjacent riparian habitats for *Ascaphus*; and 3) among-year and among-site variability in these parameters. Clearly, present methods for characterizing *Ascaphus* population size are inadequate to permit use of assessment and management methods that depend on accurate estimates of local or regional population size (e.g., population viability analysis). However, several approaches are under development.

APPENDIX TABLE 3. Summary of densities for *Ascaphus* larvae (tadpoles) from studies conducted in British Columbia, California, Oregon, and Washington. Values in red are estimates that assumed a channel width of 1 m; for the Wilkins and Peterson (2000) study, this represents a slight underestimate in densities since their mean channel width was 1.3 m.

Ascaphus species	Prov or St	Location	Time Since Harvest	Harvest Type	Density (#/m^2)				*n*	Source
					$\bar{x}$	SE	min	max		
truei	BC	Hazelton Mts.	0-15 years	Clearcut	0.34	0.08	0.0	3.1	17	Dupuis and Friele (1996) Dupuis and Steventon (1999)
			0-15 years	5-60 m Buffer	2.38	0.58	0.0	9.7	17	
			Not applicable[1]	Unharvested	1.81	0.43	0.0	4.6	18	
		Ashlu Elaho Mamquam Squamish	~5 years	Clearcut	0.98	0.55	0.36	2.08	3	Wahbe (1996) Wahbe and Bunnell (2001, 2003)
			~5 years	Buffer	2.77	-	-	-	1	
			60-80 years	Clearcut	0.67	0.09	0.58	0.85	3	
			Not applicable[2]	Unharvested	1.30	0.71	0.43	2.70	3	
		Chilliwack Skagit	<10 years	Clearcut	0.63	0.20	-	-	8	Richardson and Neill (1995) J. Richardson (*unpublished data*)[2]
			>25 years	2nd-growth	0.10	0.03	-	-	5	
			Not applicable[3]	Unharvested	0.35	0.08	-	-	7	
	WA	W slope Central Cascades	0-2 years (BACI)[4]	State Buffers	0.01	0.03	0.05	0.00	4	Kelsey (2000)[5]
			0-2 years (BACI)[4]	Modified Buffers	0.51	0.69	1.52	0.00	4	
			Not applicable[1]	Unharvested	0.35	0.40	0.84	0.02	5	
		Mt. St. Helens vicinity	Not applicable[7]	Unharvested	0.58	0.26	0.27	1.09	6	Hawkins *et al.* (1988)
			Not applicable[8]	Unharvested	4.40	2.24	1.02	8.70	3	
			Not applicable[1]	Unharvested	2.72	0.70	1.92	4.11	4	
		NF Soleduck	Not applicable[1]	Unharvested	0.52	0.45	-	-	8	Adams and Bury (2000, 2002)[6]
		Soleduck	Not applicable[1]	Unharvested	0.05	0.04	-	-	13	

Ascaphus species	Prov or St	Location	Time Since Harvest	Harvest Type	Density (#/m^2)				*n*	Source
					$\bar{x}$	SE	min	max		
truei	WA	Bogachiel	Not applicable[1]	Unharvested	0.29	0.16	-	-	26	Adams and Bury (2000, 2002)[6]
		Hoh	Not applicable[1]	Unharvested	0.20	0.30	-	-	6	
		Queets	Not applicable[1]	Unharvested	0.01	0.03	-	-	5	
		Lk Quinault	Not applicable[1]	Unharvested	0.05	0.05	-	-	11	
		NF Quinault	Not applicable[1]	Unharvested	0.23	0.19	-	-	12	
		EF Quinault	Not applicable[1]	Unharvested	0.09	0.13	-	-	6	
		Skokomish	Not applicable[1]	Unharvested	0.21	0.34	-	-	4	
		Dosewallips	Not applicable[1]	Unharvested	0.38	0.32	-	-	5	
		Gray Wolf	Not applicable[1]	Unharvested	0.90	0.49	-	-	8	
		Morse	Not applicable[1]	Unharvested	1.34	0.94	-	-	5	
		Elwha	Not applicable[1]	Unharvested	0.40	0.16	-	-	27	
		Lyre	Not applicable[1]	Unharvested	2.57	1.41	-	-	5	
		Near coastal SW WA	50-65 years	Pre-harvest - basalt	0.08	0.03	-	-	18	Wilkins and Peterson (2000)
				Pre-harvest - marine sedimentary	0.00	-	-	-	22	
		West slope of S WA Cascades	<10 years	Clearcut	0.00	-	-	-	11	Pollett et al. (2010)[10]
				Buffer	0.39	-	-	-	10	
			35+ years	Clearcut	0.20	-	-	-	10	
			Not applicable[9]	Not applicable	0.70	-	-	-	10	
	OR	Coast Range	14-40 years	Clearcut	0.37	0.21	-	-	20	Corn and Bury (1989)
			Not applicable[1]	Not applicable	0.76	0.08	-	-	23	
montanus	BC	Kootenays	various		0.9	0.2	-	-	7	Dupuis and Wilson (1999)
	OR	Wallowas	high harvest[11]		0.10	0.08	-	-	10	Bull and Carter (1996a)

Ascaphus species	Prov or St	Location	Time Since Harvest	Harvest Type	Density (#/m^2)				*n*	Source
					$\bar{x}$	SE	min	max		
montanus	OR	Wallowas	moderate harvest		0.09	0.04	-	-	10	Bull and Carter (1996a)
			low harvest[11]		0.16	0.09	-	-	10	

[1] Old-growth, stand age range unspecified.

[2] Old-growth, 250+ year old stand age.

[3] Old-growth, >250 year old stand age.

[4] Before and after control impact (BACI), two years pre- and two years post-harvest sampling, but some sites temporally staggered. Only pre-treatment densities are indicated. The measure of variation (column labeled SE) is a standard deviation.

[5] Though six sites existed in each of three treatments, five sites distributed across the three treatments were not occupied by stream-associated amphibians. The sampled sizes address only the occupied sites.

[6] In context of life stage, larval densities are an overestimate because post-metamorphic life stages were included with larvae in density estimates. All sites were within Olympic National Park.

[7] Unforested as a consequence of the May 1980 eruption of Mt. St. Helens.

[8] Lower drainage unforested as a consequence of the May 1980 eruption of Mt. St. Helens, upper drainage forested.

[9] Old-growth, 150+ year old stand age.

[10] Measure of variation not provided, but the 95% confidence interval around the estimate of the mean for each harvested category is: unbuffered (0,0), buffered (-0.1,0.7), second growth (0,0.5), and unharvested (-0.1,1.4).

[11] Level of timber harvest was determined by calculating the percentage of the landscape that drained into each stream reach sampled that had been affected by timber harvest over the last 20 years. A stream with less than 20% of the landscape harvested was classified as low, 21% to 50% harvested was moderate, and more than 50% as high. Timber harvest was defined as including clearcuts, shelterwood removals, overstory removals, and partial overstory removals within the last 20 years.

Local extirpation of populations may be a concern in the interior, and at the northern and southern range limits of *A. montanus*, given the species' low vagility and potentially high philopatric nature (see Daugherty and Sheldon 1982a). The reduced genetic diversity of south-coastal and interior populations in British Columbia compared with levels of genetic diversity in other frog species indicates that these populations may be at higher risk because of a reduced ability to respond to changing environmental conditions (Ritland *et al*. 2000). In addition, they may be less able to migrate among sites in response to changing habitat conditions because of high site fidelity (Daugherty and Sheldon 1982a; Ritland *et al.* 2000). Evidence of high genetic divergence among *Ascaphus* populations in interior watersheds compared with coastal ones is suggestive of a high level of genetic drift occurring in the interior and possibly lower fitness in these populations (Ritland *et al*. 2000). Streams in the interior of British Columbia are generally underlain with brittle, meta-sedimentary rocks and as a result contain a large proportion of fractured bedrock as mobile bedload (Dupuis and Wilson 1999). In addition, the continental climate in the interior is harsher (Dupuis *et al*. 2000). Debris torrents, summer aridity, and streambed freezing during winter probably play a significant role in local extinction and recolonization processes in this area (see Lamberti *et al.* 1991).