

Low thermal tolerances of stream amphibians in the Pacific Northwest: Implications for riparian and forest management

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Abstract. Temperature has a profound effect on survival and ecology of amphibians. In the Pacific Northwest, timber harvest is known to increase peak stream temperatures to 24°C or higher, which has potential to negatively impact cold-water stream amphibians. I determined the Critical Thermal Maxima (CT_{max}) for two salamanders that are endemic to the Pacific Northwest. *Rhyacotriton variegatus* larvae acclimated at 10°C had mean CT_{max} of 26.7 ± 0.7 SD°C and adults acclimated at 11°C had mean CT_{max} of 27.9 ± 1.1°C. These were among the lowest known values for any amphibian. Values were significantly higher for larval *Dicamptodon tenebrosus* acclimated at 14°C (\bar{x} = 29.1 ± 0.2°C). Although the smallest *R. variegatus* had some of the lowest values, size of larvae and adults did not influence CT_{max} in this species. Current forest practices retain riparian buffers along larger fish-bearing streams; however, such buffers along smaller headwaters and non-fish bearing streams may provide favorable habitat conditions for coldwater-associated species in the Pacific Northwest. The current study lends further evidence to the need for protection of Northwest stream amphibians from environmental perturbations. Forest guidelines that include riparian buffer zones and configurations of upland stands should be developed, while monitoring amphibian responses to determine their success.

Key words: Critical Thermal Maximum; *Dicamptodon*; headwater; *Rhyacotriton*; salamander; temperature.

Introduction

The Pacific Northwest of North America is home to three endemic families of amphibian that are restricted to cool-water streams: tailed frogs (Ascaphidae); torrent salamanders (Rhyacotritonidae); and Pacific giant salamanders (Dicamptodontidae). *Ascaphus* are adapted to fast, rocky streams (e.g., the larvae have a large suctorial mouth to attach to rocks) (Dupuis and Steventon, 1999; Jones et al., 2005). *Rhyacotriton* are small (few > 100 mm total length), “brook-type” salamanders that live in seeps, splash zones, waterfalls and headwaters (Nussbaum and Tait, 1977). *Dicamptodon* frequent creeks and larger streams with some in pools, and

may reach large size of up to 350 mm total length (Nussbaum et al., 1983; Jones and Welsh, 2005). *Rhyacotriton* and *Ascaphus* reach their highest numbers in older forests (Welsh, 1990; Adams and Bury, 2002) while *Dicamptodon* may also occur in more open or logged habitats (Bury and Corn, 1988; Wilkins and Peterson, 2000).

Of all the physical parameters in the aquatic environment, temperature is perhaps the most dramatic in its effect on the physiology, ecology, and behavior of anuran larvae (Ultsch et al., 1999). One of the most common responses used to quantify temperature tolerance is the Critical Thermal Maximum (CT_{max}). This index represents the temperature at which an animal loses its righting ability and would perish quickly if not removed to cooler conditions (see Hutchinson and Dupré, 1992). The CT_{max} for most anuran larvae is between 38°C and 42°C (Ultsch et al., 1999). The thermal tolerances of *Ascaphus* and *Rhyacotriton* are among the lowest known for amphibians, but data are limited in geographic scope or available for few of the species (table 1). For example, Brattstrom (1963) reported *Rhyacotriton* had a low CT_{max} ($\bar{x} = 28.3^\circ\text{C}$) but there was no mention if these were larvae or adults. He also did not state the collection site, which is important as there are now four species in the group (Good and Wake, 1992). Welsh and Lind (1996) briefly mentioned that CT_{max} tests for *R. variegatus* indicated thermal stress at 17.2°C, but they provided no other test information. I was not able to find published CT_{max} data for *Dicamptodon*.

Stebbins (1951) found field body temperatures of California *Rhyacotriton* (= *R. variegatus*) to be 5.9-9.6°C ($N = 25$). Field data of *R. variegatus* in northern California suggest that they only occur in streams where stream tempera-

Table 1. Critical Thermal Maximum (CT_{max}) of stream amphibians in the Pacific Northwest.

Species stage	N	Acclimation		CT_{max} (°C) Range	Source
		°C	\bar{x}		
<i>Ascaphus montanus</i>					
Larvae	24	10	ca. 29		Metter (1966)
Adults	12	10	ca. 28		"
	8	0	27.6		Claussen (1973)
	8	10	29.6		"
	6	20	ca. 29		"
<i>Ascaphus truei</i>					
Larvae	8	5	ca. 29.6	28.9-30.1	de Vlaming and Bury (1970)
<i>Rhyacotriton</i> sp.					
Larvae	8	13-14	ca. 28.3	27.8-29.0	Brattstrom (1963)
<i>Rhyacotriton variegatus</i>					
Larvae	7	10	26.7	25.6-27.4	This study
Adults	8	11	27.9	26.3-29.3	"
<i>Dicamptodon tenebrosus</i>					
Larvae	12	11	29.1	28.7-29.3	"

tures are $\leq 15.0^{\circ}\text{C}$ in summer (Diller and Wallace, 1996; Welsh et al., 2001; Welsh and Karraker, 2005). Brattstrom (1944) reported body temperatures of larval *Dicamptodon* (species unknown) from $12.0\text{--}16.2^{\circ}\text{C}$ ($N = 6$), and summarized field body temperatures: *Rhyacotriton*, $\bar{x} = 8.7^{\circ}\text{C}$ ($N = 28$); and *Dicamptodon*, $\bar{x} = 13.1^{\circ}\text{C}$ ($N = 12$).

Objectives of this study are to provide estimates of CT_{max} for single populations of larval and adult *R. variegatus* and larval *D. tenebrosus* from Oregon. I also summarize what is known of the thermal ecology of these two species and *Ascaphus* in relation to forestry practices that can elevate stream temperatures. Elevation of stream temperatures may pose a particular threat to *R. variegatus*, which was petitioned for listing as a Federal threatened species (U.S. Fish and Wildlife Service, 1995). Although not found to qualify for listing at that time, concerns remain about losses of *Rhyacotriton* and *Ascaphus* populations due to management practices such as timber harvest, road construction and prescribed fires.

Materials and Methods

Study animals and acclimation periods

I obtained *R. variegatus* at Parker Creek (elevation = ca. 700 m) on Mary's Peak, ca. 25 km WSW of Corvallis, Benton Co., Oregon. Measurements of snout-vent length (SVL; mm) and mass (g) of seven tested larvae were: 22 mm (0.30 g), 23 (0.38), 26 (0.55), 27 (0.54), 27 (0.61), 28 (0.57) and 32 (0.91). Adults ($N = 8$) were: male — 40 mm (1.97 g); females — 32 mm (1.06 g), 33 (1.10), 34 (1.25), 37 (1.94), 38 (1.79), 42 (1.97) and 43 (0.98). Larvae were acclimated in the laboratory at 10°C for 2-3 weeks; adults were held at $8\text{--}9^{\circ}\text{C}$ in a refrigerator and then one week at 11°C . These slight variations in average acclimation temperatures were due to changes in water inflow to the laboratory (from wells) and seasonal shifts in air temperatures.

Samples of *D. tenebrosus* larvae ($N = 12$) were from Withrow Creek (elevation ca. 790 m) near Glide, Douglas Co., Oregon, in the foothills of the Cascade Mountains. Lengths and masses were: 30 mm (1.82 g), 37 (2.92), 38 (3.15), 39 (2.95), 43 (3.52), 43 (3.90), 45 (3.77), 45 (4.25 g), 47 (4.58), 47 (5.72), 48 (5.89) and 48 (6.53). They were acclimated at 14°C (ambient water temperature) for 3 weeks.

Water for acclimation and testing was from a well near the Willamette River at Corvallis, Oregon. Photoperiod was 14 h light: 10 h dark and light intensity was $\sim 150\text{--}200$ lumens m^{-2} at the water surface. Animals were not fed during acclimation periods (2-3 weeks) because of the short time in laboratory and lack of access to natural live food sources.

Critical Thermal Maxima (CT_{max})

I defined CT_{max} of larvae as the temperature at which they exhibit uncontrolled, jerky swimming behavior or if they rolled over (belly-up) on the bottom of

the beaker. Animals were observed constantly and, once the response was clear, I poured cool water (ca. 20°C) into the beaker. This resulted in recovery with no apparent ill effects 1 week after experiments.

To prevent thermal shock, each individual was held at 20°C (1000 mL of well water in a 1-L beaker) for 10 min before each test. For larvae, water was heated with a 50-W glass-aquarium heater at an average rate of 0.6°C min⁻¹ from 20°C to the CT_{max}. Water was aerated and mixed to eliminate supersaturated gas conditions during heating. I recorded water temperature at 1-min intervals during exposure to determine the CT_{max} value. I ran control exposures under the same time and test conditions but with no heater.

I tested individual adults in an aerated 1-L beaker (with 900 mL well water), but with a screen floor (5-mm mesh; stainless steel) suspended 10 mm above the water level so that animals were in an air space above the water. A plastic Petri dish covered the beaker but a cut area allowed space for the heater, two thermometers, and a glass aeration line to enter through the top. Water was heated (and the air space above the water and screen floor) with a 50-W aquarium heater for about 20 min exposure. The air coming into the beaker through the aeration line (ca. 3 bubbles s⁻¹) was heated in a water bath to 30-35°C. Air temperature was measured at the screen floor and at the Petri dish lid, and the two values were averaged. Control exposures were conducted with the adults in the same conditions except air and water were not heated. The adults were quickly removed from the beaker when they displayed erratic behavior (e.g., twisting of body) or inability to right themselves. Animals were quickly removed and placed in cooler water (ca. 20°C) for several minutes, and then returned to holding tanks. No animals died during testing or in the control groups.

Statistical analyses

I employed a Likelihood Ratio Test (LRT) to compare the distribution of each group's scores for mass and CT_{max} (Ramsey and Schafer, 1996). The trend lines fit to each group produced a slope and y-intercept. The likelihood of parameters in a general regression model (y-intercept and slope of each group) and a reduced model (y-intercept of each group and just the larval *Rhyacotriton* data slope) were evaluated at their maximum. A *P*-value of <0.05 indicates a significant difference between the groups. I express CT_{max} as mean ± Standard Deviation.

Results

All tested animals responded similarly after ca. 15-20 min exposure to heating. Larval *R. variegatus* reached CT_{max} at 25.6-27.4°C ($\bar{x} = 26.7 \pm 0.7^\circ\text{C}$; fig. 1). The two control tests (*N* = 1 each) showed no effects (animals remained motionless or moved little). For adult *R. variegatus*, CT_{max} values were 26.3-29.3°C ($\bar{x} =$

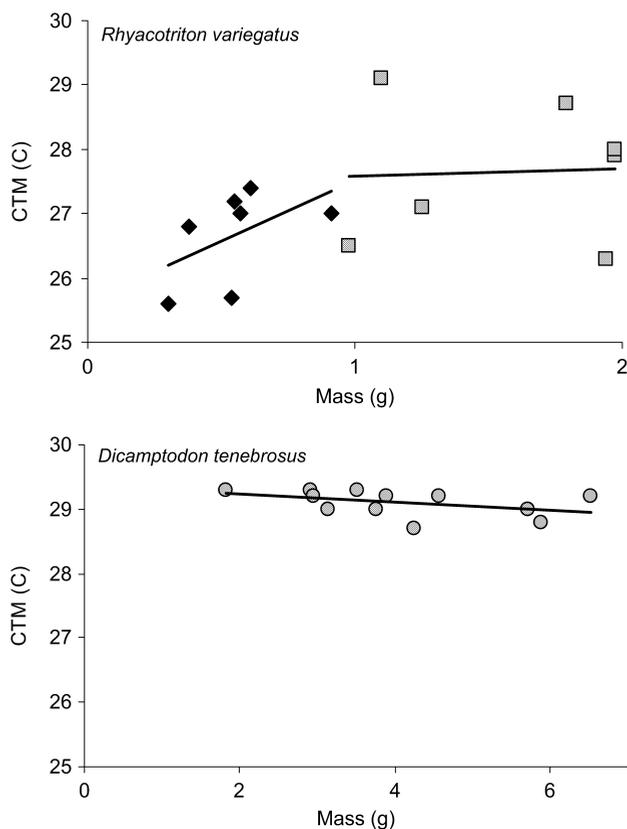


Figure 1. Critical Thermal Maxima (CT_{\max} ; °C) as a function of body mass (g). Larval southern torrent salamanders (*Rhyacotriton variegatus*) are represented by black diamonds, and adults by grey squares. Larval coastal giant salamanders (*Dicamptodon tenebrosus*) are grey circles in the lower graph.

$27.9 \pm 1.1^{\circ}\text{C}$). Three control tests ($N = 1$ each) showed no effects (animals were quiet or seldom moved).

Larval *D. tenebrosus* had statistically higher CT_{\max} ($\bar{x} = 29.1 \pm 0.2^{\circ}\text{C}$) than either group (larvae or adults) or combined data (larvae + adults) for *R. variegatus* (fig. 2). No effects occurred in two controls ($N = 1$ each).

Size of *Rhyacotriton* did not influence the CT_{\max} value (fig. 1). Larval *R. variegatus* were smaller in SVL ($\bar{x} = 26.43 \pm 2.43$ mm) and mass ($\bar{x} = 0.55 \pm 0.44$ g) than adult *R. variegatus* SVL ($\bar{x} = 37.38 \pm 4.14$ mm) and mass ($\bar{x} = 1.63 \pm 0.43$ g). Further, both were less than *Dicamptodon* in SVL ($\bar{x} = 42.5 \pm 5.50$ mm) and mass ($\bar{x} = 4.08 \pm 1.39$ g). Although the lowest CT_{\max} values were the smallest *R. variegatus*, size of animals did not influence the CT_{\max} for adult *R. variegatus* or larval *D. tenebrosus* (fig. 1). A comparison of a general regression model and a reduced model showed no significant difference between the slopes of the three groups (Likelihood Ratio Test; $P = 0.24$).

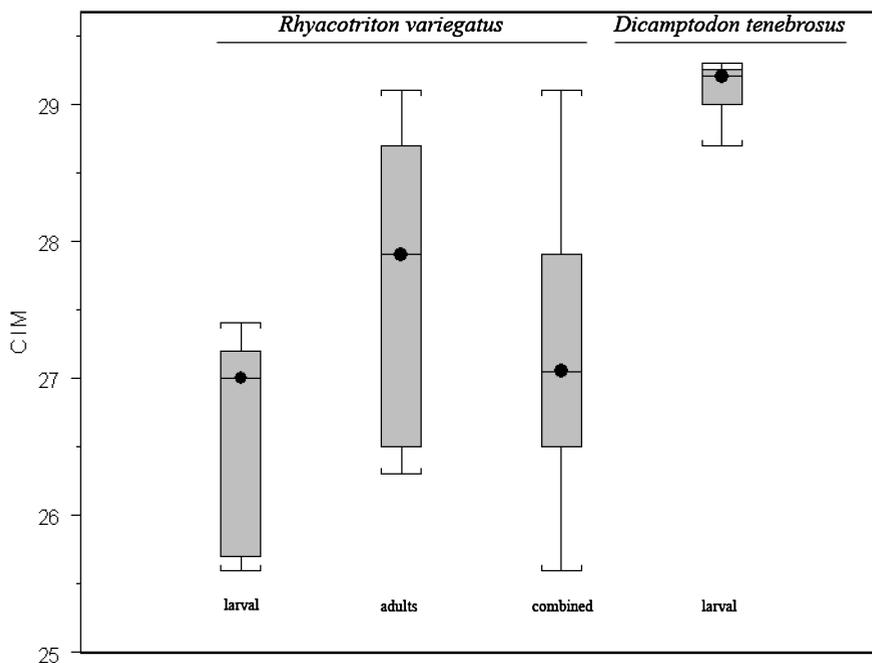


Figure 2. Critical Thermal Maximum (CT_{max}) ranges recorded for larval, adult and combined data for the southern torrent salamander (*Rhyacotriton variegatus*) and larval coastal giant salamander (*Dicamptodon tenebrosus*). Data medians for each group are represented by the black circles with bar inside each box. Boxes represent the 95% confidence interval of the data, and the associated whiskers represent the maximum and minimum data for each.

Discussion

The CT_{max} of Oregon *R. variegatus* are lower for larvae ($\bar{x} = 26.7^{\circ}\text{C}$) and adults ($\bar{x} = 27.9^{\circ}\text{C}$) than reported for any other salamander, and these values are among the lowest of any amphibian species (Brattstrom, 1963; Ultsch et al., 1999). The only lower records (CT_{max}) were for two high altitude species of Australian frogs acclimated at 5°C (Brattstrom, 1970): *Philoria frosti*, 27.1°C ; and *P. sphagnicola*, 25.8°C . Thermal tolerances of *D. tenebrosus* were higher than for *R. variegatus* (table 1). Although *D. tenebrosus* is relatively widespread in distribution and habitat, it still appears sensitive to elevated water temperatures (e.g., CT_{max} near 30°C).

The samples were progressively larger (in SVL), heavier (in g) and, apparently, higher CT_{max} from larval to adult *Rhyacotriton*, and then to larval *Dicamptodon*. However, a comparison of mass and CT_{max} for all data (no separation by species or stage) showed no statistical significance. Rather, *R. variegatus* (CT_{max} of larvae and adults combined) were different from *D. tenebrosus* (fig. 2). Within *Rhyacotriton*, most larvae had lower CT_{max} than adults but the differences were statistically insignificant. Also, greater range in mean values for adult *R. variegatus* compared to larvae may reflect the varied area within the air space for adult testing, which allowed adults to climb on the screen and up the sides of the beaker. Although Dupré

and Hutchinson (1985) reported selection of higher mean temperatures during ontogenetic shifts in larval amphibians (three anurans, one salamander), Miller and Packard (1977) reported that most evidence suggests that there was no correlation between heat resistance and body size in amphibians. I found differences between the two species of stream salamanders, but further research is required to tease out details of variation related to body size.

Alternatively, the larval *D. tenebrosus* may have had higher values because they were held at 14°C compared to *R. variegatus* larvae at 10°C and adults at 11°C. Acclimation temperatures influence CT_{max} in other amphibians, but changes are modest (range 0.7-1.8°C difference) for a 10°C change in acclimation temperature (Rome et al., 1992). Hutchison et al. (1973) found no statistical differences in CT_{max} of the stream-dwelling *Cryptobranchus alleganiensis* acclimated at 5 or 15°C but differences occurred between groups acclimated at 15°C ($CT_{max} \bar{x} = 32.99 \pm 0.40^\circ\text{C}$) and 25°C ($CT_{max} \bar{x} = 36.57 \pm 0.46^\circ\text{C}$), which is a change of 0.36°C in CT_{max} for degree⁻¹ acclimation increase. This type of response to acclimation temperature may account for the slight difference (1.2°C in CT_{max}) between the acclimation difference (3°C) between adult *R. variegatus* and larval *D. tenebrosus*.

In another cold-adapted species, Claussen (1973) reported that adult *Ascaphus* acclimated near zero temperatures had lower CT_{max} ($\bar{x} = 27.6^\circ\text{C}$) than frogs at either 10°C or 20°C acclimation ($CT_{max} \bar{x} = \text{ca. } 29.6^\circ\text{C}$). This was an average increase of 0.2°C in CT_{max} degree⁻¹ acclimation temperature from near zero to 10°C but no difference above 10°C. There are no equivalent data for any species of *Dicamptodon* or *Rhyacotriton*. Even accounting for possible influence from slightly higher acclimation temperatures, *D. tenebrosus* had a higher thermal tolerance than *R. variegatus*.

Management implications

Rhyacotriton experience the largest losses of any stream amphibian in the Pacific Northwest following clear-cut logging (Corn and Bury, 1989; Welsh and Karraker, 2005). One explanation may be absence or reduction of forest canopy after logging that result in increased stream temperatures, which may be stressful or lethal to *Rhyacotriton*. Effects appear to be ameliorated in areas with a coastal marine climate (see Diller and Wallace, 1996; Russell et al., 2004) or in small streams that have cool groundwater flows (Steele et al., 2003). In Oregon, Everest et al. (1985) stated that small streams are more subject to temperature changes (i.e., increases) than large streams.

Rome et al. (1992) reported that there is little evidence that amphibians ever experience temperatures that approach CT_{max} in nature. For *R. variegatus*, stream temperatures that are lethal ($CT_{max} = 26.7\text{-}27.6^\circ\text{C}$) may be uncommon or not experienced in forests or logged areas. Following logging or other perturbations, however, stream temperatures in summer may reach levels that are physiologically stressful to *Rhyacotriton* and *Ascaphus*. Adams and Frissell (2001) suggested that *A. montanus*

may migrate to avoid warmer parts of streams. They may be able to escape in subterranean retreats or cold seeps/springs, if available. However, stream amphibians cannot move into adjacent forests in summer or the non-rainy season as temperatures are much higher in adjacent uplands than in flowing waters or riparian zones (Chen et al., 1999).

Although CT_{max} is a standardized test of thermal tolerance by a species, it is measured with rapid increase in temperature for a short time. Summer stream temperatures at harvest units or other areas of perturbation may reach 24°C but these are usually only for 1 or more $hr\ day^{-1}$. Thus, testing species of stream amphibians under more natural patterns with fluctuating conditions (e.g., peaks at 22-24°C for 1-2 $hrs\ day^{-1}$ followed by cooling down periods to 15°C or less) would likely be more relevant to field situations.

Response to warm water for extended periods may be lethal. For example, another coldwater genus in the Pacific Northwest is *Ascaphus*. In constant water temperatures of 22°C, its larvae began to die after 24 hrs and 75% were dead after 48 hrs whereas all adults ($N = 12$) died between 18 and 30 hrs (Metter, 1966). A similar response is expected for *Rhyacotriton* because its CT_{max} is 1-3°C less than that reported for *Ascaphus*. However, such periods of extended warm water (e.g., 22°C for 12 $hrs\ day^{-1}$) are seldom encountered in the wild.

Both *Rhyacotriton* and *Ascaphus* face risk where there are elevated stream temperatures. In the Oregon Coast Range, one small stream in summer rose from 14° to 22°C at mid-day following clear-cutting of the drainage, with a peak in a pool at 30°C (Brown and Krygier, 1970). In the Oregon Cascades, Johnson and Jones (2000) reported maximum water temperatures of 23.9°C in two streams flowing through a clear-cut in a small watershed and in a stand with three small patch-cuts plus construction of logging roads. Both logged areas were burned post-harvest, which is a common forestry practice in the region. Streams in nearby mature forests did not have temperatures exceeding 19°C ($\bar{x} = 16.7^\circ C$) in summer. Temperatures in streams in logged plots did not return to the pre-harvest levels until ca. 15 yr later, coinciding with return of the riparian zone and canopy closure.

Moreover, eggs of *A. truei* die in water $> 18.5^\circ C$ (Brown, 1975). *Ascaphus* deposits its eggs in mid-summer in the warmest part of the year and, thus, face stress immediately. *Rhyacotriton* appears to deposit eggs in spring and early summer, and it may take 200 d for hatching (Nussbaum and Tait, 1977; Nussbaum et al., 1983). Currently, we lack any data on the thermal tolerance of the eggs of *Rhyacotriton*.

Perturbations caused by natural (e.g., wildfires) and human (e.g., timber harvest) events in the Pacific Northwest may cause elevated stream temperatures to levels of 24°C or more in summer. These have potential to stress or harm cold-adapted species such as stream amphibians. Similar to salmonid fishes of the Pacific Northwest (Carline and Hachung, 2001), *Ascaphus* or *Rhyacotriton* rarely occur in streams that have water temperatures $> 16^\circ C$ (Welsh, 1990; Diller and Wallace, 1996; Welsh et al., 2001). In Oregon streams, Huff et al. (2005) reported that stream amphibians were consistently found in streams with low temperatures

(averages): larval *Dicamptodon* (12.0-14.3°C) and *Ascaphus* (11.7-15.3°C). Some *Ascaphus* have been found in streams with water temperatures up to 21°C where groundwater seeps create cold pockets and spatially complex thermal environments (Adams and Frissell, 2001). Recently, Dunham et al. (2007) report *A. montanus* occurring in streams with a maximum daily peak in summer up to 26°C but most waters (54%) were cooler (<20°C). Sites in burned, reorganized stream beds had a high probability (>0.75) of exceeding 20°C whereas streams in unburned areas were low (<0.25). Although stream amphibians may occur in relatively warm waters for brief periods (e.g., >24°C for 1-2 h), the animals may be compromised (e.g., have reduced agility, feeding, and growth rates). However, these potential sublethal effects of thermal stress on these amphibians remain unstudied.

To provide suitable habitat conditions for coldwater species, several authors (see Vesely and McComb, 2002; Bury, 2004; Sarr et al., 2005; Olson et al., 2007) recommend buffer zones along headwaters and around seeps to provide shade and reduce sedimentation from management activities. These are now prescribed to protect fish habitat on larger streams (Beschta et al., 1987; Hawkins et al., 1983; Sedell and Swanson, 1984), but are inconsistently applied across geographic regions (Olson et al., 2007) or rare on non-fish bearing streams (see Sheridan and Olson, 2003). Current forest practices increasingly recommend or require riparian buffers along headwaters and small streams (see Bury, 1994; de Maynadier and Hunter, 1995; Diller and Wallace, 1996). These are critical steps toward maintenance of stream conditions and adjacent riparian habitat favorable to amphibians and other forest wildlife. Moreover, many forests have multiple perturbations and landscape effects such as salvage logging occurring after wild fires (Pilliod et al., 2003; Odion and Sarr, 2007) or are a mosaic such as logged habitat upstream of old-growth forests (Corn and Bury, 1989; Biek et al., 2002). It will be important to understand the responses of amphibians and other forest wildlife to these complex interactions. Headwaters, streams and riparian buffers (e.g., 10-25 m wide) should only cover a fraction (e.g., 5-10%) of the land area in most Pacific Northwest forests (Bury and Corn, 1988). However, we lack information on the most effective buffer widths to protect these sensitive riparian zones, which are critical to the survival of cold-adapted species such as *Rhyacotriton* and *Ascaphus*, and salmonid fishes.

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