THE EFFECTS OF NEARSHORE FOREST THINNING ON UPLAND HABITAT USE BY

POND-BREEDING AMPHIBIANS IN A MONTANE CONIFEROUS FOREST

By

ANDREW HOLT MCINTYRE

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The members of the Committee appointed to examine the thesis of ANDREW

HOLT MCINTYRE find it satisfactory and recommend that it be accepted.

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Jonah Piovia-Scott, Ph.D., Chair

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Cheryl Schultz, Ph.D.

_____

Jesse Brunner, Ph.D.

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Abstract

by Andrew Holt McIntyre, M.S.
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Chair: Jonah Piovia-Scott

Forest thinning removes woody fuels from coniferous forests in a way that mimics

historic wildfire regimes by removing mid-story pines and increasing horizontal and vertical

spacing. Thinning results in few long-term effects to habitat features required by sensitive

amphibians including canopy cover, soil moisture and available cover objects. Though some

research suggests minimal effects of thinning to amphibians, few studies have assessed effects to

aquatic-breeding amphibians in forests of the Pacific Northwest. We conducted an experimental

study evaluating effects of understory thinning on aquatic-adjacent habitat on forest conditions

and amphibian movement patterns. Thinning treatments were implemented in 12 plots,

alternating with matching controls, in the pine-fir forests surrounding Big Lake, a 10.7 ha

ephemeral lake in northern California. We assessed effects of thinning on habitat variables

relevant to amphibians and used pitfall traps to assess movement by long-toed salamanders

(*Ambystoma macrodactyllum*), western toads (*Anaxyrus boreas*), and Pacific chorus frogs

(*Pseudacris regilla*). We investigated associations between amphibian captures and upland

habitat conditions and assessed amphibian use of debris piles created during treatments. We

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predicted metamorphic amphibians would seek cover and shade in control plots, while adults would find migration easier in treated plots. Tree density decreased while woody debris cover showed a moderate increase after treatments. A modest increase in captures of chorus frogs occurred in treatment plots, but no treatment effect was detected for toads or salamanders. Receding surface waters forced salamander larvae to develop and emerge at the eastern end of Big Lake. With a shorter development time, western toads and chorus frogs were able to emerge from the pond before surface waters receded. Salamanders and chorus frogs were captured in areas of high leaf litter and low tree density, suggesting a preference of these species for foraging in lower intensity forests. Foraging diurnally, toads preferred areas offering high levels of canopy cover. Our results suggest moderate understory thinning in forests adjacent to aquatic habitat may show no harmful short-term impacts to pond-breeding amphibians. No amphibians were found under debris piles; future research should survey such piles during different times of year and directly before burning.

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CHAPTER ONE

FUEL TREATMENTS: EFFECTS ON HABITAT CONDITIONS AND

AMPHIBIANS IN UPLAND CONIFEROUS FORESTS

Introduction

Wildfires in coniferous forests have become larger and more devastating over the last 30 years, particularly across the western United States. Over 10 million acres of US forests were burned by wildfires in 2015, more than a 50% increase over the preceding decade (US Department of the Interior 2016). Prior to the 20th century, fires in coniferous forests of North America were small in scale and had a burn frequency of roughly 3-50 years (Whitlock et al. 2003). Yet two centuries of fire suppression activities interrupted this pattern; a lack of small, frequent fires has led to coniferous forests thick with deciduous undergrowth and mid-story pine-fir stands (Agee and Skinner 2005; Pilliod et al. 2003; Stephens 1998; Whitlock et al. 2003). Thick understory growth leads to increased fuel loads for fires and allows small ground fires a stepwise connection to the canopy, turning small sparks into largescale fires (Agee and Skinner 2005; Pilliod et al. 2003). The number of wildfires increased during the 1980's and 1990's while fires increased notably in size over the past two decades (Abatzoglou and Williams 2016; Garman et al. 2001; Nagy et al. 2018; Naughton et al. 2000). As wildfires have historically been linked to years with higher temperatures (Abatzoglou and Williams 2016; Whitlock et al. 2003), climate projections describe increasing temperatures and more extreme droughts over the coming decades (Cayan et al. 2008; Fettig et al. 2013; Franco et al. 2011; Moritz et al. 2012). Anthropogenic sources of ignition are also on the rise as a result of population growth, suburban sprawl and outdoor recreational activities (Abatzoglou and Williams 2016; Prestemon et al.

2013). This combination of fuel-heavy forests, dry conditions and increased ignition sources has produced larger and more devastating fires than at any period in recent history (Keyser and Westerling 2017; Moritz et al. 2012; Prestemon et al. 2013).

Forest managers attempt to combat this increased fire risk by removing excess fuels from fire-suppressed forests to simulate historic fire regimes (Agee and Skinner 2005). State and federal agencies across the United States increase implementation of these 'fuel treatments' on publicly managed lands each year; currently almost 3 million acres per year at treated (Cochrane et al. 2012; Stone et al. 2010; US Department of the Interior 2016). Fuel treatments reduce fire risk by increasing crown spacing and removing understory and mid-story growth from coniferous forests (Agee and Skinner 2005; Pilliod et al. 2003; Pollet and Omi 2002). Forest managers employ three main types of fuel treatments. Clearcutting increases spacing between forest patches; yet knowledge of its destructive effects on local ecology has led to a decrease in its use on both public and private land in recent decades (Garman et al. 2001; Naughton et al. 2000; Stone et al. 2010; Ryan et al. 2013). Prescribed fire best mimics the effects of small-scale fires by removing small undergrowth from forests (Pilliod et al. 2003; Ryan et al. 2013). Thinning treatments remove mid-story stands and shrubs and offer forest managers versatility of intensity and implementation options (Pilliod et al. 2003; Pollet and Omi 2002). Thinning has emerged as the most effective method of reducing fuels while retaining forest integrity in coniferous forests (Butler et al. 2012; Pilliod et al. 2003).

As thinning treatments reduce the risk of wildfire, they have the potential to affect habitat conditions in local forests such as canopy cover, leaf litter inputs and soil conditions such as soil moisture content, temperature and compaction (Matthews at al. 2010; Pilliod et al. 2003; Pilliod et al. 2006; Verschuyl et al. 2011). Post thinning research focuses on fuel loads and often

neglects effects to wildlife, especially within riparian, aquatic and wetland-adjacent habitat (Pilliod et al. 2003; Pilliod et al. 2006; Verschuyl et al. 2011). Amphibians that breed in aquatic systems within coniferous forests often spend most of their lives in upland forested habitat where they require specific microhabitat conditions and are sensitive to changing conditions (Gardner et al. 2007; Madison and Farrand 1998; Semlitsch 1983). This sensitivity to habitat change is a major factor leading to declines in amphibian populations across North America (Gardner et al. 2007; Hof et al. 2011; Piovia-Scott et al. 2016). As both public and private forest managers implement thinning treatments across more acres of forest each year, thinning will play an important role in amphibian conservation over the coming decades (Stone et al. 2010).

The goal of this review is to summarize effects of fuel treatments on habitat conditions and amphibians within upland coniferous forests of North America. I will assess effects of fuel treatments to various life stages of amphibians focusing on effects within aquatic-adjacent habitat. Research in this area has focused on terrestrial and stream-breeding species habituating the southeastern United States; few studies have focused on pond-breeding species, particularly across western North America. The main types of forest treatments will be compared in terms of effects on local habitat conditions and occupancy and abundance of local amphibians. The review will conclude by acknowledging research gaps in this field that need to be addressed.

Background

Amphibians

Amphibians play important ecological roles within aquatic ecosystems, aquatic-adjacent habitat and upland coniferous forests. Amphibians act both as top-down predators and important prey for larger vertebrates, thus playing a vital role in carbon cycling within local food webs

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(Ågren et al. 2008; Davic and Welsh 2004; Hopkins 2007; Vitt et al. 1990; Wake 1990). In aquatic systems, larval amphibians feed on detritus, diatoms and aquatic invertebrates, converting primary productivity and aquatic biomass into energy and carbon stores (Davic and Welsh 2004; Dodd 2010; Hopkins 2007). Amphibian eggs and larvae often occur on the order of tens of thousands of individuals within one aquatic system, providing a massive source of energy to local food webs (Piovia-Scott et al. 2016). In terrestrial habitats, adult and juvenile amphibians affect leaf litter depth and soil-forming processes through top-down control of fossorial and ground-dwelling invertebrates (Best and Welsh 2014). Amphibians also contribute large amounts of energy to food webs within upland habitats, acting as important prey for reptiles, mammals and birds (Best and Welsh 2014; Piovia-Scott et al. 2016). Carbon flows heavily from upland forests to lowland aquatic habitats; amphibians represent a major flow of energy and nutrients from wetlands back into upland areas (Piovia-Scott et al. 2016).

Terrestrial amphibians, as well as the juvenile and adult life stages of aquatic-breeding amphibians, require specific habitat conditions in upland coniferous forests. Species at higher latitude or elevation require overwintering opportunities in the form of subterranean tunnels, rock crevices and mammal burrows (Pilliod et al. 2003; Semlitsch et al. 2009; Verschuyl et al. 2011; Wells 2010). Such tunnels are only available where soil matrices are soft and moist, allowing mammals to burrow several feet below the surface (Mcgraw 1998; Moghaddas and Stephens 2008; Searcy et al. 2013). A complex soil matrix provides moisture and regulated temperatures that aid homeostasis as well as providing an array of terrestrial and fossorial invertebrate prey and predator avoidance opportunities (Anderson 1968; Wells 2010). Herbaceous growth and fallen woody debris also provide shelter and microhabitat needed for homeostasis, foraging and predator avoidance (Madison 1997; Pilliod et al. 2003; Semlitsch et al.

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2009; Verschuyl et al. 2011). Homeostasis is more easily managed in areas with high levels of overstory canopy cover and a high-water table (Pilliod et al. 2003; Verschuyl et al. 2011). Many of these habitat conditions are provided by early successional habitats and were historically maintained by regular, small-scale wildfires (Garman et al. 2001; Hossack and Pilliod 2011; Stephens 1998).

The need for very specific habitat conditions has made amphibians a group of conservation concern across a North American continent that has seen dramatic changes to coniferous forests over the last two centuries (Grant et al. 2016; Odum 1985; Wake 1990; Welsh and Ollivier 1998). Marked declines of amphibian populations were first noted on a global scale beginning in the 1950's, and current estimates describe a 3-4% annual loss of amphibians globally (Grant et al. 2016). This decline is attributable to numerous threats that often work additively, including land-use change, pathogens, invasive species, non-native fish, pollutants and climate change (Gardner et al. 2007; Gibbons et al. 2000; Hof et al. 2011; Houlahan et al. 2000). In North America, pathogens such as *Batrachochytrium dendrobatidis* and *Ranavirus* have resulted in notable amphibian declines in recent decades (Olori et al. 2018; Yap et al. 2018). Invasive species such as bullfrogs and trout act as both competitors and predators of native aquatic amphibians (Miro et al. 2018; Viers et al. 2013; Yap et al. 2018). Yet land use-change is often identified as the largest culprit of amphibian decline across North America, and as development and fuel treatments affect millions of acres of coniferous forests each year, they pose a serious threat to amphibians in coniferous forests and adjacent aquatic systems (Gardner et al. 2007; US Department of the Interior 2016).

Wildfires and Fuel Treatments

Coniferous forests of western North America have a history of small, frequent wildfires that can be traced back over two-thousand years (Heyerdahl 2001; Sweetnam 1993). Though fire intervals vary over time, fire scar evidence indicates that fires have occurred less frequently over the last 150 years as a result of human development (Abatzoglou and Williams 2016; Stephens 1998; Sweetnam 1993). In previous centuries, wildfires removed undergrowth and young tree stands, leaving coniferous forests dominated by large, fire-resistant pine and fir species (Whitlock et al. 2003). Fires created a forest landscape with horizontal spacing between large canopy-level pines as well as bimodal vertical spacing via large vertical gaps between dominant pines of the canopy and low forest scrub (Agee and Skinner 2005; Stephens 1998). Before human influence, coniferous forest landscapes included large, fire resistant pine and fir species dominating the canopy, early successional herbaceous and woody growth on the forest floor, and large gaps between canopy trees (Stephens 1998). Mid-story pine groves were only found in large forest gaps that had been created by treefalls and were isolated from canopy trees (Agee and Skinner 2005; Stephens 1998; Whitlock et al. 2003).

Around 150 years ago, anthropogenic fire suppression began a shift in fire regime as a result of overgrazing of cattle, timber harvests of fire-resistant arboreal species, and direct fire suppression activities (Heyerdahl et al. 2001; Stephens 1998; Sweetnam 1993; Whitlock et al. 2003). Undergrowth that had once been burned regularly began to blossom, increasing stands of young and mid-aged pines that connected scrub on the forest floor to the tallest pines in a ladder-like manner (Agee and Skinner 2005; Pilliod et al. 2003). The presence of these mid-sized 'ladder fuels' allowed small ground-level sparks to progress to the forest crown, creating fires with the potential for largescale destruction (Skinner and Taylor 2006; Pilliod et al. 2003). As

fire suppression increased through the 19th and 20th century, wildfire occurrence decreased while forests became choked with dense thickets of ladder fuels (Whitlock et al. 2003). Increased fuel loads allowed small fires to burn longer and hotter, often growing into largescale, devastating fires. The combination of increased fuel loads, increased in temperatures and anthropogenic sources of ignition, today's coniferous forests are more prone to large, devastating wildfires than at any point in history (Keyser and Westerling 2017; Moritz et al. 2012; Prestemon et al. 2013; Westerling and Bryant 2008).

To combat this fire risk, forest managers have turned to fuel treatments with the goal of returning coniferous forests to a more historic state (Agee and Skinner 2005). By 2010, 43% of forest managers across the United States were conducting some form of fuel treatment (Stone et al. 2010). Clearcutting, prescribed fire and thinning all reduce fuel loads and increase crown spacing, create forest gaps and promote vertical bimodality by removing undergrowth and mid-story stands (Agee and Skinner 2005). Management objectives include reducing single-aged stands and protecting large fire-resistant pines (Agee and Skinner 2005). Fuel treatments result in a decrease in vertical and horizontal connectivity between trees, preventing small sparks from reaching the forest crown and preventing crown-level fires from spreading (Stephens 1998; Whitlock et al. 2003). Clearcutting affects forest connectivity, fundamentally changing local habitat conditions and proving a less sustainable approach to fuel removal (Ryan et al. 2013; Stephens 1998). Prescribed fires efficiently remove low-growing vegetation and shrubs, though implementation neglects mid-story growth and necessitates treating forests on a small scale (Ryan et al. 2013). Thinning treatments promote both vertical and horizontal spacing, targeting removal of individual trees from the canopy as well as removing mid-story stands (Pollet and Omi 2002; Ryan et al. 2013). Thinning reduces fuel loads while maintaining the integrity of local

ecosystems and has emerged as the most practical method of fuel reduction in coniferous forests in the 21st century (Butler et al. 2012; Pilliod et al. 2003).

Fuel Treatments

Clearcutting

Clearcutting, or stand-level harvests, use mechanical methods to remove all trees from designated areas (Bowyer et al. 2009; Garman et al. 2001). Though clearcutting is often used by private landowners for tree harvests, it is also used by public land managers as a method of fuel reduction. Clearcutting of coniferous forests often results in single species stands followed by a quick regeneration (20-80 years) of the same species (Garman et al. 2001). Spatial heterogeneity and successional patterns are often lost as even-aged stands provide little habitat variation (Bowyer et al. 2009; Garman et al. 2001). This management approach removes fuel in the form of live trees and woody debris, creating large openings in the forest that do not accurately represent previous forest conditions (Kirkland et al. 1996). Though clearcutting successfully reduces the risk of wildfires (Franklin and Forman 1987; Lindenmayer et al. 2006; Nitschke 2005), it significantly alters ecosystem functioning and drastically impacts local wildlife.

Clearcutting results in reductions in both vertical and horizontal habitat complexity that do not accurately replicate effects of historic wildfire regimes, removing almost all canopy cover for a period of many years after implementation (Garman et al. 2001; Grialou et al. 2000; Maigret et al. 2014; Petranka et al. 1994). Habitat for tree dwellers and foragers is decreased (Garman et al. 2001), along with microhabitat opportunities in the form of woody debris on the forest floor (Garman et al. 2001; Semlitsch et al. 2008). Canopy reductions affect soil conditions, increasing sun exposure to the forest floor and leading to warmer, drier soils (Tilghman et al.

2002; Semlitsch et al. 2009). Tree removal reduces litter inputs to soils, impacting soil formation and dynamics (Grialou et al. 2000). Clearcutting that uses heavy machinery for implementation may also compact soils and increased erosion, fundamentally changing soil structure (Petranka et al. 1994; Semlitsch et al. 2009). The effects of clearcutting reach beyond treated plots as edge effects may extend over 200m into nearby forests and wetlands (Chen et al. 1995; Jones et al. 2018; Witt et al. 2013; Maxell 2000).

Evidence suggests stand-level fuel treatments result in a decrease in amphibian activity and in some cases have rendered local ecosystems completely inhospitable to sensitive pond-breeding species (Garman et al. 2001; Lindenmayer et al. 2006; Stephens 1998). Significant declines in amphibian abundance and occupancy have been noted in clearcuts when compared to either untouched (deMaynadier and Hunter 1995; Todd et al. 2009) or thinned areas (Karraker and Welsh 2006), especially among terrestrial salamanders (Knapp et al. 2003; Maigret et al. 2014; Petranka et al. 1994). In a meta-analysis considering effects of forest treatments on terrestrial salamanders, Tilghman et al. (2012) found a 50-62% reduction in abundance within clearcut areas relative to control plots. Clearcuts have also been linked to a decrease in amphibian body size, weight and overall health (Peterman et al. 2011; Powell and Babbitt 2015). Mechanisms of decline include a loss of woody debris (Maguire et al. 2005), increased soil temperature and decreased soil moisture resulting from reduced canopy cover (Semlitsch et al. 2009). Amphibians that do not emigrate from clearcut areas are forced to increase time spent seeking cover, affecting time available for foraging, breeding and migrations (Tilghman et al. 2012). Site occupancy may be retained if clearcut areas offer amphibians supplementary shelter, such as high density of mammal burrows (Rothermal and Luhring 2005) or woody debris (Semlitsch et al. 2008). Clearcutting results in negative effects to local habitat conditions and

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wildlife; its use has notably declined in both the public and private sectors in recent years (Stone et al. 2010).

Prescribed Fire

By the late 20th century, prescribed fire had become the most frequently used method of fuel treatment for forest managers across North America (Pilliod et al. 2003). Prescribed fires mimic historic fire regimes by reducing forest undergrowth, regenerating early successional habitat and producing small openings within forests (Maxell 2000; McLeod and Gates 1998; Olson 2000; Pilliod et al. 2003; Russell et al. 1999). In contrast to many of the largescale wildfires seen today, prescribed fires are tightly controlled, burning at a size and temperature that simulate historic small-scale fires (Pilliod et al 2003; Schurbon and Fauth 2003). Most burns are completed outside of the dry summer months when fire risk is highest and instead are implemented after rains during spring and fall months when the forest floor contains a higher moisture content, allowing for a cooler, more controlled burn (Bishop and Haas 2005). Prescribed burns offer understory removal with less destructive effects to local habitat conditions than largescale wildfires that burn at very high temperatures (Russell et al. 1999).

Prescribed fires reduce overgrown pine stands and undergrowth, renewing early successional patterns and increasing structural complexity within coniferous forests (Brockway and Lewis 1997; Cain et al. 1998; Kirkland et al. 1996; Russell et al. 1999). Burns may initially reduce leaf litter cover (Greenberg and Waldrop 08; McLeod and Gates 1998); long-term differences in litter depth only occur after extremely hot fires or burns that are repeated in quick succession (Schurbon and Fauth 2003). Though fires often remove existing debris from the forest floor, the burning of small brush and undergrowth adds new debris inputs to the forest floor

(Harmon et al. 1986; Maxell 2000). Soil temperatures increase initially after burns and may stay elevated as a result of increased sun exposure (Hossack et al. 09; Schurbon and Fauth 2003). Burns may also affect aquatics by increasing short-term water temperature, sedimentation rates and changing water chemistry and flow rates due to changes in topsoil dynamics and water retention ability (Dunham et al. 2007; Minshall et al. 1997; Pilliod et al. 2003; Rieman and Clayton 1997; Russell et al. 1999; Schurbon and Fauth 2003). Yet changes to soil dynamics and aquatic habitats after prescribed burns are often short-lived (Johnson and Jones 2000; Schurbon and Fauth 2003).

The effects of prescribed fires to amphibians have rarely been assessed outside of the southeastern United States. Yet evidence suggests amphibians in coniferous forests can cope with habitat changes resulting from small wildfires and prescribed fire. Declines in amphibian occupancy and abundance often involve large wildfires that burn at high temperatures, affecting species that are highly vulnerable to changes in conditions on the forest floor (McLeod and Gates 1998; Hossack et al. 2009; Hossack and Pilliod 2011). Direct mortalities are almost never observed in either upland or aquatic habitat (O'Donnell et al. 16; Smith 2000; Pilliod et al. 2003). Most literature notes little to no change in abundance or body condition following prescribed fires or low intensity wildfires in both southeastern (Ford et al. 1999; Greenberg and Waldrop 2008; Greenberg et al. 2018; Kilpatrick et al. 2004; Moseley et al. 2003; Perry et al. 2009) and northwestern coniferous forests (Arkle and Pilliod 2010; Bury 2004; Dunham et al. 2007). Amphibians that require very cool, moist soils may show an initial decrease in abundance, especially if burns are repeated within a short time frame (Hossack et al. 2009; Schurbon and Fauth 2003). Yet species that are well-adapted to regular wildfires and early successional habitat may increase in abundance due to an increase in foraging and basking habitat (Brown et al. 2011,

Brown et al. 2014; Dunham et al. 2007; Greenberg and Waldrop 2008; Hossack and Corn 2007).

Though amphibian surface activity may decrease in the short-term after prescribed burns (Greene

et al. 2016; Ford et al. 2010; O'Donnell et al. 2015; O'Donnell et al. 2016; Schurbon and Fauth

2003), long-term site occupancy is usually not affected (Arkle and Pilliod 2010; O'Donnell et al.

2016).

Effects of prescribed fire on amphibians varies based on habitat type, burn intensity and

timing of burn as well as the niche and vagility of the amphibian species (Pilliod et al. 2003).

Amphibians that are habitat generalists, late-season breeders or are highly active on the forest

surface are at a greater risk of harm (Klaus and Noss 2016; Maxell 2000; Pilliod et al. 2003).

Most wildfires occur during warm mid-summer months when amphibians are sheltered in

subterranean burrows, under cover objects or within aquatic habitats where they can avoid harm

from low intensity fires on the forest floor (Maxell 2000; Schurbon and Fauth 2003). Risk of

harm increases when prescribed burns are implemented during times when local amphibians are

foraging, breeding, or migrating (Bishop and Haas 2005; Pilliod et al. 2003). Planning prescribed

fires when local amphibians are not active on the forest floor may help retain site occupancy

(Bishop and Haas 2005). Burn frequency also affects long-term occupancy as implementing

multiple burns in quick succession (1-3 years) significantly affects leaf litter content, woody

debris, soil moisture and temperature (Matthews et al. 2010; Schurbon and Fauth 2003).

Thinning

Thinning treatments (a.k.a. partial harvests, understory removal) are implemented in a

variety of ways based on goal crown height, basal density and exact method of implementation

(Pollet and Omi 2002). Rather than removing all trees from an area, thinning focuses on reducing

ladder fuels by removing shrubs and mid-story tree stands (Agee and Skinner 2005). Some

thinning treatments increase horizontal tree spacing by removing a select number of large trees

from the forest canopy while others focus on increasing vertical spacing by reducing mid-story

stands (Agee and Skinner 2005; Pollet and Omi 2002). Thinning changes coniferous forests in a

way that simulates historic fire regimes while still reducing the risk of largescale fires (Agee and

Skinner 2005; Pilliod et al. 2003). Thinning treatments maintain a higher degree of habitat

integrity and ecosystem functioning than clearcuts, yet still change habitat conditions within

local coniferous forests (Hocking et al. 2013; Verschuyl et al. 2011).

Most research notes a loss of total canopy cover after thinning treatments (Matthews et

al. 2010; Pilliod et al. 2003; Pilliod et al. 2006), though losses are not as severe as are observed

after clearcuts (Maigret et al. 2014; Semlitsch et al. 2009). Thinning treatments open early

successional opportunities and promote growth of young shrubs and ground vegetation that

increase ground cover of the forest floor (Anderson and Poage 2014; Suzuki 2000; Verschuyl et

al. 2011) and can compensate for losses in canopy cover by retaining local soil moisture levels

(Anderson and Poage 2014; Suzuki 2000; Verschuyl et al. 2011). Though some research notes

losses in leaf litter and woody debris cover after thinning (Suzuki 2000; Thompson et al. 2003;

Verschuyl et al. 2011), others note either no effects to leaf litter and cover objects or a quick

return to pretreatment levels within a few years' time (Anderson and Poage 2014; Greenberg et

al. 2018; Rota et al. 2017).

Many of the specific habitat conditions required by amphibians are not affected by

thinning treatments. Moderate and lower-impact thinning (ie. hand-thinning) do not compact

soils or affect the density of mammal burrows and subterranean refugia available as shelter

(Madison 1997; Osbourn et al. 2014). Thinning maintains the diversity, richness and total

abundance of arthropod prey in forested uplands (Anderson 1968; Apigian et al. 2006). Young

pine stands absorb large amounts of water; their removal maximizes local groundwater levels at

an intermediate level of tree cover (Hossack and Pilliod 2011; Ilstedt et al. 2016; Jones et al.

2018). Thus, removal of excess undergrowth in wetland-adjacent areas increases the hydroperiod

of local wetlands, allowing aquatic-breeders more time for development. The removal of excess

trees and shrubs may expedite migration and foraging activity of terrestrial amphibians

(Anderson 1967; Howard and Wallace 1985; Trenham and Shaffer 2005). In a review of thinning

treatments, Verschuyl et al. (2011) noted that, "biophysical characteristics necessary for moisture

sensitive amphibian species may still be retained in thinned forests."

Evidence points to limited effects of thinning treatments on both abundance and site

occupancy of amphibians in coniferous forests. Literature noting minimal effects of thinning to

local amphibians have been noted across North America including the Northeast (Brooks 1999;

McKenney et al. 2006), the southern Appalachia region (Ford et al. 2000; Kilpatrick et al. 2004;

Steen et al. 2010), and the Northwest (Grialou et al. 2000; Raphael et al. 2002). Similar results

have been noted specifically in pond-breeding salamanders as abundance and species richness is

often unaffected by thinning treatments (Kilpatrick et al. 2004; Grialou et al. 2000; Patrick et al.

2008). Initial decreases in abundance or surface activity often rebound in 5-10 years (Anderson

and Poage 2014; Morneault et al. 2004; Rota et al. 2017) while long-term assessments often

yield comparable numbers in terms of site occupancy and abundance relative to pretreatment

plots (Aubry 2000; Kluber et al. 2008). A threshold effect for shade cover has been noted

following thinning treatments, as post treatment site occupancy may depend on retaining a

specific level of canopy cover (Skelly et al. 2005; Williams et al. 2008). In a review of effects of

fuel treatments on 33 species of pond-breeding amphibians, Semlitsch et al. (2009) found

clearcutting had an overwhelming negative effect on amphibian abundance while partial harvests often resulted in no effect or even an increase in amphibian abundance.

Effects of thinning on amphibian populations often differ by the type of thinning, local habitat conditions and the life history strategy of amphibians (Pilliod et al. 2006). For example, the ability of anurans to store water in their bladder allows them to cope with losses of canopy cover and soil moisture better than most salamander species (deMaynadier and Hunter 1995; Todd et al. 2009). Species that are nocturnal, move only during rain events, or frequent subterranean tunnels and mammal burrows are often able to avoid increased warming on the forest floor (Pilliod et al. 2006). Pond-breeding salamanders require more canopy cover and soil moisture than more terrestrially breeding species (Bunnell and Dupuis 1999; Jacobs and Houlahan 2011) while terrestrially breeding salamanders, such as ensatina (*Ensatina eschscholtzii*), require high levels of habitat complexity and woody cover for breeding and may suffer after treatments that remove excess woody debris (Verschuyl et al. 2011). Within thinned plots in western Oregon, Olson and Burton (2014) noted declines in abundance of the coastal giant salamander (*Dicamptodon tenebrosus)*, a species requiring moist upland habitat. Yet an increase in abundance was noted for Dunn's salamander (*Plethodon dunni*) and several *Rhyocotriton* species in the same plots, reflecting their ability to cope with lower moisture levels (Olson and Burton 2014). Responses to thinning may also differ by life stage. As emergent amphibians spend most of their first year in riparian and wetland-adjacent areas, requiring high moisture levels to maintain homeostasis (Semlitsch 1998), thinning in these areas may result in decreases in local juvenile abundance and may force young to travel longer distances to find desired shelter (Homyack and Haas 2009; McGraw 1998; Todd et al. 2014).

New Forestry

By the late 1980's, the effects of high-impact fuel treatments on local ecosystems and wildlife had became apparent. Land managers realized the long-term effects of clearcutting and heavy thinning and began to see a divergence between wildlife conservation and harvest quotas and fuel reduction goals (Garman et al. 2001; Naughton et al. 2000; Stone et al. 2010). At this time, management goals across the Pacific Northwest and northern Rocky Mountains shifted, attempting to balance harvest goals with maintaining ecological diversity and local conservation (Carey and Curtis 1996; Polis 1997; Stone et al. 2010; Suzuki 2000; Swanson and Franklin 1992). Termed 'New Forestry,' these contemporary forest management practices first included leaving a few large trees within clearcut areas and altering harvesting rotations to leave tree stands of differing ages on the landscape, thus increasing vertical habitat complexity (Hansen et al. 1995).

More recently, alternative forestry practices leave woody debris along the forest floor to help maintain soil dynamics and create microhabitat opportunities for wildlife (Swanson and Franklin 1992). New Forestry treatments leave patches of trees separated by large gaps in the forest (Naughton et al. 2000; Swanson and Franklin 1992). Such fuel treatments disconnect individual patches enough to prevent the spread of large wildfires while still providing both edge and mid-forest habitat to a variety of wildlife (Swanson and Franklin 1992). Non-traditional thinning methods that leave irregularity in terms of tree spacing, canopy height and harvest intensity reduce fire risk and increase habitat complexity (Garman et al. 2001). Most state and federal agencies have established protocols that leave riparian areas (often termed 'Streamside Management Zones') as buffers between treatment areas and stream habitat, though this protection is not designated equally to aquatic systems (Maigret et al. 2014; Witt et al. 2013).

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The benefits of leaving buffer zones around stream and aquatic systems still needs more research (Gorman et al. 2013). In contrast to fuel treatments that focus on fuel removal and timber harvests, most contemporary fuel treatments minimize their impacts to local wildlife.

Alternative methods of fuel removal often result in no effect or even an increase in abundance and site occupancy of local amphibians. Thinned plots augmented with additional woody debris often note no decline in abundance of local amphibians (Brooks 1999; Suzuki 2000). Rundio and Olson (2007) found a 40% decrease in Ensatina (*Ensatina eschscholtzii*) and Western Red-backed Salamanders (*Plethodon vehiculum*) after traditional thinning treatments in headwater streams in western Oregon; no such decrease in abundance was detected in plots left with riparian buffers or woody debris augmentation. Implementation of these 'Streamside Management Zones' in conjunction with nearby clearcuts and thinning treatments can alleviate declines of local amphibians (deMaynadier and Hunter 1995; Harpole and Haas 1999; Hawkes and Gregory 2012; Homyack and Haas 2009; Maigret et al. 2014; Perkins and Hunter 2006). Canopy cover retention is a particularly beneficial aspect of alternative thinning treatments. Treatments that leave higher levels of understory shrub cover (Rundio and Olson 2007; Suzuki 2000) or overstory canopy cover (Brooks 1999; Knapp et al. 2003; Hocking et al. 2013; Maigret et al. 2014) maintain higher amphibian abundance when compared to traditional clearcut or thinned plots. Though management of fuel treatments is a continually shifting dynamic, modern thinning practices balance fuel removal with sustainability and may maintain occupancy and abundance of local wildlife while still reducing the risk of largescale wildfires.

Conclusion

Forest managers of the 21st century face the difficult task of balancing management goals that include timber harvests for profit and reducing fuels to prevent largescale wildfires with promoting conservation of local wildlife species. Amphibians play a key role in coniferous forest and aquatic ecosystems, but their susceptibility to changes in local habitat conditions make them a high conservation priority for forest managers. Clearcutting effectively reduces woody fuels but mimics the effects of largescale fires, leaving local habitat conditions unsuitable for most amphibians. Clearcutting may be used on private land but has proven an inviable option for most public land managers addressing local conservation issues.

Prescribed fire and thinning more accurately reflect the effects of historic fire regimes by reducing fuels while still maintaining high levels of ecosystem functioning in coniferous forests. Both methods maintain the majority of overstory cover while opening early successional habitat and increasing habitat complexity. Most amphibians habituating coniferous forests are well-adapted to small-scale fires and benefit in a variety of ways from moderate increases in forest openings. Yet implementation of prescribed fire is limited by the need to tightly control burn size, frequency and time of year, and does not provide forest managers with sizeable timber yields. Thinning may be implemented with a variety of goal densities and allows managers the flexibility to reduce fuels, collect modest levels of timber and still provide habitat complexity that facilitates conservation goals. Evidence suggests both prescribed fire and thinning maintain habitat conditions that allow for the persistence of amphibian populations. Over the last three decades, 'New Forestry' techniques, including lower impact thinning and the leaving of buffer zones and woody debris have proven most effective at creating habitat complexity and meeting local conservation goals. These methods of forest management maintain or even promote local

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abundance of woodland amphibians. Thinning and New Forestry techniques provide the highest levels of flexibility needed for future fuel treatments and should be favored by forest managers seeking to maintain local wildlife diversity.

As the importance of removing fuels and conserving wildlife both increase, a paucity of research exists concerning effects of fuel treatments to pond-breeding amphibians of western North America (Pilliod et al. 2003; Pilliod et al. 2006). Yet most research in this area has been conducted in the short term (1-2 years) and may not accurately reflect persistence over time. Future research should address long-term abundance and occupancy levels and focus on effects across seasons; fuel treatments implemented during periods of amphibian activity may amplify effects and may need to be managed on a local scale. Additional research is needed concerning guidelines for the leaving of riparian 'buffers zones' in wetland-adjacent areas. Often these management zones do not accurately mimic historic fire regimes, leaving riparian habitat choked with understory growth and mid-story pines. Research into long-term effects of these buffer zones on amphibian populations of western North America is quite lacking. Prescribed fire and thinning treatments better reflect historic fire regimes; implementation of these treatments adjacent to aquatic habitat should be considered as an alternative to the leaving of buffer zones.

CHAPTER TWO

THE EFFECTS OF NEARSHORE FOREST THINNING ON UPLAND HABITAT USE

BY POND-BREEDING AMPHIBIANS IN A MONTANE CONIFEROUS FOREST

Introduction

Wildfires have increased in size and intensity on a global scale over the last half century as a result of climate change, fire suppression, and an increase in anthropogenic sources of ignition (Abatzaglou and Williams 2016; Agee and Skinner 2005; Westerling 2016; Whitlock et al. 2003). This trend has led to a global rise in forest management practices aimed at removing woody fuels from forests with the specific goal of reducing wildfires, especially in temperate forest regions where areas of concentrated woody fuels often abut centers of human development (Abatzaglou and Williams 2016; Cochrane et al. 2012; Stone et al. 2010). Understory thinning treatments effectively reduce the occurrence of largescale fires in coniferous forests and are projected to increase in use as a means of fire prevention over the coming decades, particularly in areas that have recently experienced largescale fires, such as western North America (Agee and Skinner 2005; Butler et al. 2012; Gorman et al. 2013; Swanson and Franklin 1992). Despite extensive research on the effectiveness of understory thinning in reducing fuels and fire risk, less research exists evaluating effects of these treatments to wildlife. Few studies assess effects of thinning on species that traverse the boundary between forests and adjacent aquatic habitats (Bisson et al. 2003; Pilliod et al. 2003; Pilliod et al. 2006).

Aquatic-adjacent forest ecosystems form a sensitive transition zone between upland habitat and aquatic systems and provide critical habitat for numerous sensitive species (Pilliod et al. 2003; Semlitsch et al. 2009; Verschuyl et al. 2011). Though forest managers have included

ecologically significant stream-breeding species into management goals for decades (ie. Salmonidae spp.; Fausch et al. 2009), persistent knowledge gaps have prevented pond-breeding species from receiving the same consideration. Forest managers continue to take a 'hands-off' approach within aquatic-adjacent areas, leaving buffer zones adjacent to wetlands that do not mimic historic fire regimes and may not provide amphibians with preferred habitat conditions (Bisson et al. 2003; Brosofske et al. 1997). Identifying specific needs of sensitive species in these aquatic-adjacent habitats will provide insight into the use of aquatic-adjacent buffers for amphibian conservation within coniferous forests.

Pond-breeding amphibians living in forest ecosystems offer a unique opportunity to study the effect of fuels management on sensitive aquatic systems as they use both aquatic habitat for breeding and upland forests for shelter and foraging. Amphibians are the most threatened vertebrate group in North America and are highly vulnerable to changes in upland forest conditions (Grant et al. 2016; Wells 2010; Welsh and Droege 2001; Welsh and Hodgson 2013). Breeding and development occurs in aquatic areas; yet pond-breeding amphibians spend most of their lives foraging and seeking shelter in upland forests (Blaustein 1994; Petranka 1998; Viers et al. 2013; Wells 2010). Amphibians select upland habitat based on the need to regulate body temperature and skin moisture, and escape predation (Pilliod et al. 2003; Wells 2010). Amphibians seek shade provided by overstory canopy cover, cover objects in the form of woody debris and a deep leaf litter matrix, and soft, moist soils that offer refuge in the form of subterranean mammal burrows (Anderson 1968; Pilliod et al. 2003; Semlitsch et al. 2009; Verschuyl et al. 2011). Though many pond-breeding amphibians of western North America are adapted to historic fire regimes, fuel treatments may alter habitat in ways that do not mimic

historic fires and may have important consequences for sensitive amphibians (Franco et al. 2011; Schmidt et al. 2008; Semlitsch et al. 2009; Westerling and Bryant 2008).

Most understory thinning treatments preserve the upland habitat characteristics required by sensitive aquatic-dependent species by maintaining pretreatment levels of coarse woody debris, moderate levels of canopy cover as well as conserving soil integrity (Greenberg et al. 2018; Rota et al. 2017; Schurbon and Fauth 2003). Thinning removes mid-story trees and increases shrub production on the forest floor, thus increasing habitat complexity and soil moisture (Anderson and Poage 2014; Verschuyl et al. 2011). Groundwater levels increase after thinning, raising soil moisture and inputs to local aquatic systems (Hossack and Pilliod 2011; Ilstedt et al. 2016). Yet, despite the apparent maintenance of habitat integrity, assessments of amphibian abundance and activity after thinning treatments have found mixed results. Although initial decreases in amphibian abundance have been noted after thinning treatments (Anderson and Poage 2014; Morneault et al. 2004; Rota et al. 2017), most long-term studies have found abundance is often unaffected over time (Aubry 2000; Kluber et al. 2008). Several studies have found no significant effect of thinning on amphibian occupancy or abundance (Grialou et al. 2000; Karraker and Welsh 2006; Raphael et al. 2002). Patterns often show species-specific results, sometimes yielding both positive and negative responses by different species in the same study (Olson and Burton 2014; Semlitsch et al. 2009). Many of these studies suggest responses to understory thinning vary with specific life history strategies connected to local ecosystem processes. Research on effects of thinning to pond-breeding amphibians of western North America has been conducted over a limited range of species and geographic areas; entire regions, such as the southern Cascades/Sierra Nevada ecoregion, are devoid of such research.

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We conducted an experimental study to evaluate the effects of understory thinning treatments on movement patterns and upland habitat use of three amphibian species at Big Lake, an ephemeral lake located in the pine-fir forests of Lassen National Forest in northern California. The upland habitat immediately adjacent the lake (within 30-60 m) consists of thick stands of young pines and fallen debris that was deemed a Riparian Conservation Area during a previous thinning project and was left unaltered. To assess the effects thinning in this nearshore area will have on amphibians, hand-thinning and piling treatments were implemented in 50 m wide plots alternating with adjacent controls in the upland forest surrounding the lake. Drift fence arrays complete with pitfall traps were erected in upland forests and used to assess movement of three resident amphibian species: long-toed salamanders (*Ambystoma macrodactyllum*), western toads (*Anaxyrus boreas*), and Pacific chorus frogs (*Pseudacris regilla*). Amphibians were collected in traps during a pilot year (2017), during the summer months and the fall migration period for one year prior to treatment (2018) and during one fall migration period following treatment (2019). We conducted habitat surveys before and after treatments to evaluate changes to upland habitat. Plot choice and habitat preferences observed for amphibians after treatments may project an opportunity for sustained abundance and survival following understory thinning treatments in aquatic-adjacent habitat. We also uncovered several debris piles collected during treatments to evaluate their use as cover by migrating amphibians. We hypothesized that capture rates of metamorphic amphibians would be highest in control plots as amphibians are most vulnerable to desiccation and predation during their first year (Patrick et al. 2008; Semlitsch 1998) and will seek out areas providing the most canopy cover and woody debris. In contrast, we expect capture rates of adult amphibians would be highest in treated plots where the removal of trees, large

woody debris, and other obstacles would facilitate migrations across upland habitat. Amphibians of all three species were expected to utilize debris piles as cover objects during fall migrations.

Methods

Study System

Our study was conducted at Big Lake, an ephemeral lake located at 1,800 meters in the Hat Creek Ranger District in Lassen National Forest (Figure 1). Big Lake is a shallow, silt-bottom lake that receives most of its water from snow-pack runoff and is fed by a spring and several seeps located on the north side of the lake. The lake dries throughout the summer, leaving minimal surface water by late summer/early fall and revealing a meadow habitat complete with a variety of forbs, grasses and sedges. Vegetation in the forested uplands surrounding the lake consists primarily of pines (lodgepole, ponderosa, and sugar) and firs (red and white). Long-toed salamanders, western toads, and Pacific chorus frogs use the lake for breeding activities in the spring and larval development throughout the summer. As annual dry-down prevents colonization by fish, Big Lake acts as important habitat for long-toed salamanders, a California state species of special concern that is highly susceptible to fish predation (Kenison et al. 2016; Pearson and Goater 2009). Adult amphibians frequent the forested uplands surrounding Big Lake throughout much of the year; newly metamorphosed young retreat to forested uplands in late summer and early fall. Much of the uplands surrounding Big Lake was mechanically thinned by the US Forest Service in 2016. The first 30-60 m of upland habitat immediately surrounding the lake was left as a Riparian Conservation Area; it now consists of thick stands of young lodgepole pines, fir trees and downed woody debris (Figure 2A).

Experimental Design

We divided the uplands surrounding Big Lake into twenty-six 50 m wide plots that extended 60 m outward from the lake meadow (Figure 1). We used these 50 m wide plots as the unit of treatment, thinning a total of 12 plots while leaving 14 plots as controls in an alternating control/treatment design. Rocky conditions in two consecutive plots on the eastern end of the lake left treatment difficult; thus, they were left as consecutive control plots. We did not treat the west and northwest ends of the lake.

Treatments specifications were outlined in the 'Big Lake Thin and Pile' project sponsored by the US Forest Service (agency code 10106) and were implemented by the California Conservation Corps over the course of three weeks from mid-July through mid-August of 2019. Within treated plots, trees under a 10 in. (25.4 cm) diameter were hand-thinned in a feathering pattern at a density of 10 ft by 10 ft (3 m by 3 m) in the first 20 m adjacent to the lake meadow, a density of 15 ft by 15 ft (4.5 m by 4.5 m) in the next 20 m transitioning into a density of 20 ft by 20 ft (6.1 m by 6.1 m) up to 60 m from the lake meadow (Figure 2B). Treatments were implemented in all plots up to a minimum of 30 m from the lake; some plots required treatments up to 60 m from the lake based on goal density requirements. We collected large debris from treatments as well as selected existing woody debris under 15 in. (38.1 cm) in diameter into piles within treated plots (Figure 2C). Piling did not include woody debris in the meadow, debris above 15 in. (38.1 cm) in diameter, or debris that was significantly decayed. Piles were comprised almost entirely of wood from lodgepole pines, red firs and white firs. We collected 8-20 debris piles in each treatment plot, averaging 4-8 m in diameter and 1-2 m in height. We assembled piles a minimum of 50 ft (15.2 m) from the lake meadow; some piles were

placed past the rear boundary of the treated plot into the previously treated forest. Control plots were not disturbed during treatment implementation.

Pitfall Traps

To assess the effect of thinning treatments on movement of amphibians in upland habitat, we erected drift fence arrays complete with pitfall traps in the plots surrounding Big Lake during the 2018 (pretreatment) and 2019 (post treatment) seasons. We installed three traps in each plot at distances of 3 m, 30 m and 60 m from the lake meadow for a total of 78 traps (Figure 1). Traps erected in 2018 and 2019 followed an identical layout. In 2018, traps were opened during select weeks from late May through mid-August, as well as one week in both September and October (Appendix A). Low capture rates early in the season and in between rain events in 2018 emphasized the need to open traps during late-season rain events. Thus, we did not open pitfall traps until after treatment implementation in early August of 2019; they were kept open during most of August, September, and during one week in mid-October. We installed 94 pitfall traps during a pilot year in 2017 in locations unique to that year; traps were opened during several weeks in August and one week in September. We used trap captures from this year for analysis of upland habitat associations. Statistical analyses used amphibian captures occurring during metamorphic emergence and fall migrations; captures from spring and early summer months were left out of analysis due to low capture rates. The survey dates used in analysis were defined for each species as any day after the beginning of metamorphic emergence where at least one individual of that species was captured. This date corresponded to 15 June for western toads, 1 July for Pacific chorus frogs, and 1 August for salamanders. For analysis, we defined survey period as one continuous 1-2 week trip to Big Lake when traps were opened.

Drift fence arrays included a section of shade cloth fencing 5 m long and roughly 45 cm high held in place by 5 wooden stakes. We positioned fences facing the lake meadow; the bottom 6 cm of fencing were buried to prevent amphibians from passing underneath fences. We placed pitfall traps at each end of the fence; these consisted of a large tin can buried in the ground covered by a cedar plank cover board (Dodd 2010). Plastic collars were placed inside the cans to prevent salamander escape while a hanging string helped aid escape of incidental rodent captures (Karraker 2001). Each tin contained a sponge and was refilled with water daily to maintain moist conditions in the trap. We checked and repaired pitfall traps daily during active sampling periods.

We recorded all captures of vertebrates by species and life stage; all animals were quickly released under a nearby log or bush. Amphibians were classified into three life stages including newly metamorphosed young (metamorphosed in that year), subadults and adults. To avoid affecting recapture probability, amphibians were not released under logs located directly behind or in front of traps. Traps that were significantly damaged overnight by wildlife or heavy rains were marked 'unavailable' and treated as closed for the day in analyses. Early observations indicated water levels in Big Lake recede to the far eastern portion of the lake throughout the summer. As the location of late-season water may influence the location of larval development, emergence and subsequent pitfall trap captures, the straight-line distance from the location of late-season water (Figure 2D) to the front of each plot was recorded (termed 'distance to late-season water') and included in analysis on a per-trap basis. We also included the distance of each trap to the lake (termed 'distance to lake') in analyses.

Habitat Assessments

       To assess upland habitat characteristics, we conducted four randomly generated 5 m radius vegetation surveys in each of the 50 m wide plots and a 2.5 m radius vegetation survey at each trap location. We conducted surveys July-August of 2018 and repeated them in the same locations post treatment in August of 2019. Wasp nests prevented repeating four of these surveys in 2019. As plot locations were not determined until 2018, vegetation surveys in 2017 were only completed at trap locations. We recorded leaf litter depth and percent woody debris cover as indicators of cover available for amphibians in upland habitat. Leaf litter depth was assessed from the top of the litter to the beginning of hard-packed soil; measurements were made to the nearest centimeter with a standard ruler. Five leaf litter depth measurements were taken and averaged for each plot. We assessed woody debris cover on a percent ground-cover basis (ranging 1-70%) during each survey; debris piles located within habitat plots in 2019 counted towards percent woody debris cover. We used tree density and canopy cover as indicators of shade cover, an important factor in maintaining soil moisture and reducing temperatures on the forest floor (Pilliod et al. 2003). All trees that reached breast height were tallied and divided by the total survey area (per m^2). We assessed canopy cover measurements via a spherical densiometer on a scale of 1-17, converting results into percent cover values. We took four canopy measurements during each survey, each while standing in the middle of the 5 m radius plot facing each of the four cardinal directions. Canopy cover measurements were then averaged for each plot. We also recorded slope using a clinometer to measure the gradient between the highest and lowest point in each plot.

Debris Pile Surveys

We assessed debris pile use by amphibians via five debris pile surveys conducted on the afternoon of 18 October 2019. Surveys were conducted during the fall migration period; a heavy rain event led to the capture of 181 amphibians in pitfall traps on the morning of 17 October and another 60 amphibians on the morning of pile removal. Piles were located in various treatment plots on the north, east and southeastern portions of the lake where pitfall trap captures indicated high levels of amphibian activity. We surveyed piles located 15-45 m from the lake, between 3-4.5 m in diameter and 1-2 m in height; traps were not located in the direct vicinity of pitfall traps (Figure 2C). Debris pile surveys included removing individual logs until the entire pile was disassembled and remade in a nearby location. All leaf litter and cover objects located beneath the pile were searched for amphibians.

Statistical Analyses

To evaluate the effect of thinning treatments on upland habitat conditions we ran a multivariate analysis of variance test comparing habitat characteristics in control and treatment plots post treatment (2019). The predictor variable was treatment; response variables included averages of the plot-level habitat values collected during the 5 m radius vegetations surveys and included tree density, woody debris cover, canopy cover and leaf litter depth. We log-transformed tree density and standardized each of the four response variables using a Z score transformation (Clark-Carter 2014). We used the Shapiro-Wilks test to assess multivariate normality of dependent variables and Levene's test to confirm that the assumption of equal variances. To confirm that pretreatment habitat conditions were not significantly different across plot type, we ran a preliminary MANOVA test assessing differences in pretreatment habitat

conditions (2018) between control and treatment plots. We log-transformed leaf litter depth in this analysis; otherwise the analysis was identical to the post treatment analysis. Test results confirmed that pretreatment habitat conditions were not significantly different across plot type. All statistical analyses were done using program 'R' version 3.4.1 (R Core Team 2013).

To evaluate the effect of thinning treatments on upland habitat use by amphibians, we used generalized linear mixed models to evaluate differences in trap-level captures between control and treatment plots. We ran four separate models; one for metamorphic chorus frogs, western toads and long-toad salamanders as well as one for adult long-toed salamanders. There were not enough captures to model subadults of any species or adult chorus frogs or western toads. The response variable in these models was amphibians caught in each individual trap during each survey period post treatment. The fixed predictor variables included treatment, each trap's straight-line distance to the location of late-season water ('distance to late-season water') and each trap's distance to the lake. We also tested for possible interactions between treatment and the two distance variables. We included trap-level pretreatment capture rates (2018) as a predictor for each species and life stage to account for pre-existing variation in activity patterns. Capture rates were calculated as the number of amphibians captured in 2018 divided by the sampling effort, also referred to as trap-days, or the total number of days each trap was open during the survey period (unopened or unavailable traps were removed). We included the number of trap-days for each trap in each survey period in 2019 as an offset to account for variation in survey effort. Plot, trap, and survey period were included as random effects. We ran models with a Poisson error distribution and a log link function using the 'glmmTMB' command in the {glmmTMB} package in program R (Brooks et al. 2017). We used the {performance} package (Lüdecke et al. 2020) to assess overdispersion and included an observation-level

random effect to account for issues of overdispersion in all models except for salamander adults (Harrison 2014). The significance of fixed effects was evaluated using likelihood ratio tests; interaction terms were removed from the model to assess the main effect of treatment.

For analysis of associations between amphibians and upland habitat conditions we used generalized linear mixed models to assess the relationship between pitfall trap captures and seven upland habitat variables. We ran separate model-fitting exercises for five categories of amphibians: (i) long-toed salamander adults, (ii) metamorphic long-toed salamanders, (iii) metamorphic Pacific chorus frogs, (iv) metamorphic western toads, and (v) metamorphic long-toed salamanders captured after peak emergence (after 20 September). We ran this last model in anticipation that emergence by metamorphic salamanders is likely related to the location of late-season water and may obscure associations with other habitat variables. The response variable in these models was the total number of individuals caught in each trap aggregated over each survey period across all three survey years. We grouped the fixed predictor variables into four categories: (i) distance to late-season water, (ii) forest characteristics (tree density and canopy cover), (iii) soil characteristics (leaf litter depth and woody debris cover), and (iv) habitat geometry (slope and distance to lake) (Table 3). All habitat characteristics were taken from the trap-level vegetation surveys; we log-transformed tree density and standardized each of the four response variables using a Z score transformation (Clark-Carter 2014). We included the number of trap-days for each trap in each period as an offset to account for effort; plot, trap, and survey period were included as random effects. We ran models with a Poisson error distribution and a log link function using the 'glmmTMB' command in the {glmmTMB} package in program R (Brooks et al. 2017). We ran all possible combinations of the 4 categories of predictor variables (15 total models for each species and life stage), ranked them using Akaike information criterion

corrected for small sample size (AICc), and calculated model weights (Burnham and Anderson 2002). We assessed the importance of variables using a Chi-squared likelihood ratio tests for the top ranked model for each species and life stage.

Results

Habitat Conditions

The MANOVA on post treatment habitat conditions revealed a significant effect of treatment on overall habitat conditions ($F_{4,21}=10.32$, $P<0.001$). Tree density was 68.5% lower in treated plots than in control plots ($F_{1,24}=31.04$, $P<0.001$; Figure 3) while percent woody debris cover was 23.6% higher in treated plots ($F_{1,24}=3.88$, $P=0.06$). We did not detect a significant effect of treatment for either leaf litter depth ($F_{1,24}=2.49$, $P=0.13$) or canopy cover ($F_{1,24}=0.36$, $P=0.55$).

Long-toed Salamanders

We captured 5,174 long-toed salamanders in pitfall traps including 9 adults, 16 subadults and 216 metamorphic young in 2017, 325 adults, 43 subadults and 41 metamorphic young in 2018, and 465 adults, 19 subadults and 4,040 metamorphic young in 2019. A treatment effect was not detected for pitfall trap captures of either adult or metamorphic long-toed salamanders (Table 1; Figure 4). The top model for associations of habitat conditions and adult salamander captures did not include distance to late-season water. Captures of adult long-toed salamanders showed a positive association with canopy cover and leaf litter depth while a negative association was found for tree density and woody debris cover (Table 2). Captures of

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metamorphic long-toed salamanders were most correlated with the location of late season water; a negative association was detected with woody debris cover and tree density.

Captures of adult long-toed salamanders declined sharply with distance to lake: 72.5% of adults were captured 3 m from the lake while only 13% reached traps located 60 m from the lake. Though captures of metamorphic salamanders declined notably with distance to lake, 53% of captures occurred 30 m or more from the lake with 26.5% of captures occurring 60 m from the lake. When modeling metamorphic salamanders captured post emergence, the distance to late-season water was not in the top model (Appendix B). The only notable difference in habitat associations in the model containing captures of metamorphic salamanders post emergence was a decrease in the association with woody debris cover.

Western Toads

We captured 1,404 western toads in pitfall traps including 1 adult, 11 subadults and 586 metamorphic young in 2017, 9 adults, 2 subadults and 7 metamorphic young in 2018, and 5 adults, 28 subadults and 755 metamorphic young in 2019. We did not detect a treatment effect for pitfall trap captures of metamorphic western toads (Table 1; Figure 4). Captures showed a positive association with canopy cover, a negative association with distance to lake and distance to late-season water, and a marginally significant negative association with leaf litter depth (Table 2).

Pacific Chorus Frogs

We captured a total of 3,577 Pacific chorus frogs in pitfall traps including 3 adults, 2 subadults and 335 metamorphic young in 2017, 76 adults, 7 subadults and 590 metamorphic

young in 2018, and 52 adults, 1 subadult and 2,511 metamorphic young in 2019. We detected a marginally significant positive treatment effect ($\chi^2_{(1)}$=3.04, P=0.08) as well as a marginally significant treatment by distance to lake interaction effect for pitfall trap captures of metamorphic Pacific chorus frogs ($\chi^2_{(1)}$=2.81, P=0.09); chorus frogs were captured closer to the lake in treatment plots than in control plots. Captures of chorus frogs showed a significant positive association with leaf litter depth and a negative association with tree density, distance to lake and woody debris cover (Table 2). The top model for Pacific chorus frogs did not include distance to late-season water.

Debris Piles

A detailed search beneath five debris piles on 18 October 2019 revealed no long-toed salamanders, western toads, or Pacific chorus frogs using debris piles as cover.

Discussion

We hypothesized that post treatment captures of metamorphic amphibians would be highest in control plots as young amphibians would seek plots offering the highest levels of canopy cover and woody debris. The absence of a treatment effect for metamorphic long-toed salamanders and western toads may reflect the fact that treatment did not significantly change canopy cover, woody debris or leaf litter depth; emergent amphibians had access to ample shade and cover objects within treated plots. It may also suggest understory thinning treatments implemented adjacent to aquatic zones may not affect abundance or survival of long-toed salamanders or western toads immediately following treatments. Adults salamanders stayed close to the lake in the fall; with a choice of habitat type they showed no preference in plot type.

More metamorphic Pacific chorus frogs were captured in treatment plots related to controls, potentially reflecting a preference for foraging in lower intensity upland forests. Long-toed salamanders and Pacific chorus frogs avoided thick pine-fir stands and may receive initial benefits from the removal of overgrown tree stands surrounding breeding ponds if major ground disturbance is avoided during treatments. Captures of metamorphic long-toed salamanders suggest emergence of amphibians that require long hydroperiods will occur in upland habitat surrounding areas of late-season water.

Treatment Effect

We did not detect differences in abundance of long-toed salamanders or western toads in treated plots relative to controls. Aside from a decrease in tree density, differences in important habitat features were not detected in treated plots relative to controls. Fuel treatments usually do not result in direct mortalities of amphibians but instead alter local habitat conditions in a way that leave amphibians more susceptible to desiccation or predation, resulting in either mortalities from exposure or emigration (Harper et al. 2008; Russell et al. 1999). Decreases in local amphibian abundance after thinning treatments are associated with forest floor disturbance (Morneault et al. 2004; Verschuyl et al. 2011), a loss of woody debris (Olson and Burton 2014) or a decrease in canopy cover (Anderson and Poage 2014; Morneault et al. 2014; Naughton et al. 2000). Such disturbances are often associated with mechanical thinning and piling treatments that degrade soils and necessitate heavier thinning to allow room for large machines (Morneault et al. 2004; Thompson et al. 2003). Treatments at Big Lake were implemented via chainsaws and were able to preserve leaf litter depth, removing only understory trees and leaving overstory pines that provide shade cover. Though tree density decreased after treatments, such declines

have only been associated with a decrease in amphibian abundance when treatments are heavy enough to reduce canopy cover (Greenberg et al. 2018). Understory thinning treatments within aquatic-adjacent habitat may not affect abundance or survival of long-toed salamanders or western toads in the short-term when treatments result in minimal ground disturbance or changes to other upland habitat conditions.

The lack of a treatment effect is particularly notable for adult long-toed salamanders that stay in proximity to the lake during fall migrations; most adult salamander captures (72.5%) occurred 3 m from the lake during September and October. Adults near the lake had their choice of plot type post treatment and did not show a preference for either plot type. Treatment plots may offer adult long-toed salamanders equal opportunity for foraging and seeking cover during the fall migration period when compared to controls.

The effect of treatment differed by species as capture rates of Pacific chorus frogs tended to be higher in treated plots relative to controls. Pacific chorus frogs are partial to low intensity forests that provide both shade and emergent vegetation rather than high intensity stands (Goldberg and Waits 2009; Goodman and Johnson 2011; Leonard et al. 1993; Riley et al. 2005). Emergent frogs are often found 1-1.5 meters off the ground in shrubbery during the months after first emergence (Marnell 1997). In the heavily wooded northwest, chorus frogs seek early successional forests (Raphael 1988), previously thinned stands (Goldberg and Waits 2009), and even open wetland habitats adjacent clearcuts (Bosakowski 1999). Capture rates at Big Lake reflect this preference for low intensity stands and, as thinning treatments usually promote growth of emergent vegetation (Anderson and Poage 2014), suggest that thinning of thick pine stands adjacent to breeding ponds may benefit Pacific chorus frogs. A treatment by distance to lake effect suggests chorus frogs forage in treated plots in August and September but seek

control plots for overwintering; the removal of existing woody debris in treated plots may mean control plots offer more large, decayed logs as cover objects for overwintering. In the high Sierras, Pacific chorus frogs overwinter in underground shelters (Bradford 1989) and locate overwintering grounds by early fall (Schaub and Larson 1978). By late September, young frogs that have reached traps located 30-60 m from Big Lake may shift priorities from foraging to seeking shelter for overwintering. As large, weathered logs were collected into debris piles during treatments, control plots may offer better cover objects for overwintering frogs.

Upland Habitat Associations

Though habitat associations varied by species, some general conclusions may be drawn regarding upland habitat associations of amphibians at Big Lake. With the exception of western toads, pitfall trap captures of all species and life stages showed a negative association with tree density (Table 2). Dense forest stands offer amphibians cool, moist soils as a result of increased canopy cover and leaf litter depth (Naughton et al. 2000; Pilliod et al. 2003; Semlitsch et al. 2009). Yet thick, overgrown pine-fir stands may offer physical impediments to migrating amphibians and little in the way of habitat diversity for foraging (Goldberg and Waits 2009; Lee-Yaw et al. 2014), especially for chorus frogs that are known to forage near shrubs and emergent vegetation (Goldberg and Waits 2009). Despite avoiding thick tree stands, salamanders and chorus frogs moved through habitat offering high levels of leaf litter, reflecting previous findings that these species use deep leaf litter matrices for cover and homeostasis (Dodd 2010; Maxell 2000; Welsh and Lind 1991). Results from Big Lake suggest pond-breeding amphibians may receive initial benefits from the thinning of thick, overgrown tree stands close to breeding ponds if moderate levels of leaf litter depth are maintained.

Habitat analysis surprisingly showed a negative association of captures of all species and life stages with woody debris cover. Western toads, Pacific chorus frogs, and long-toed salamanders all use woody debris for cover and foraging when in upland habitat (Anderson 1967; Maxell 2000; Pilliod et al. 2003). Amphibians in coniferous forests prefer cover objects that have seen several seasons of weathering and decay, providing microhabitat and higher moisture levels over the surrounding habitat (Pilliod et al. 2006; Welsh and Hodgson 2008; Welsh and Ollivier 1998). Though our coverboards may offer solace to amphibians in habitat devoid of cover objects, they may select larger, more decayed logs and stumps in areas offering more woody debris, thus decreasing capture rates in local traps. Given the extensive evidence that pond-breeding amphibians use woody debris as cover in upland forests, results are unlikely to indicate an aversion to habitat providing high levels of woody debris cover.

Distinctive habitat associations for western toads may result from a foraging strategy that differs from the other two species. A positive association was found between toad captures and canopy cover (Table 2). Unlike long-toed salamanders and chorus frogs that forage at night and seek shelter below ground during daylight hours (Beneski et al. 1986; Claussen 1973), western toads often forage diurnally on the forest floor (Bartelt 2000; Livo 1998; Smits 1984). Metamorphic toads are susceptible to desiccation and seek cool, moist foraging grounds that provide high canopy cover during daylight hours (Livo 1998; Wright and Wright 1949). We did not detect an association between tree density and toad captures, suggesting young toads are not deterred by foraging in thick tree stands. Toads are known to forage in a wide variety of habitats (Smits 1984; Wright and Wright 1949) and may show no inclination to avoid thick pine stands. An alternate foraging strategy may mean western toads do not receive the same benefits from thinning as species that forage in lower density forests.

Orientation of Amphibian Movements in Upland Forests

Captures of newly metamorphosed long-toed salamanders were strongly influenced by the proximity of pitfall traps to late-season water. Water levels in Big Lake recede towards the eastern end of the lake throughout the summer; by late July, this end of the lake holds 2-3 feet of water while most other sections of the lake offer shallow water or are completely dry. Larval ambystomatids prefer deep, cool waters (Bancroft et al 2008; Guderyahn et al. 2016) and require at least a 10-week hydroperiod for full larval development (Beneski et al. 1986; Howard and Wallace 1985). Receding water levels force larval salamanders into the eastern portion of the lake by July (Figure 1; Figure 2D) in a way comparable to observations of Yosemite toad (*Anaxyrus canorus*) larvae (Sherman and Morton 1993). When showers arrived in August and September (unpublished manuscript), thousands of young salamanders emerged into upland habitat surrounding the eastern portion of the lake, increasing capture rates in local traps without showing a preference for treatment type. As temperatures and the occurrence of drought increase across western North America (Cayan et al. 2008; Franco et al. 2011), the hydrology of high elevation wetlands will affect channel morphology and microhabitat in wetland systems (Lowry et al. 2010; Null et al. 2010). Seasonal dry-downs will funnel late-developing amphibian larvae into areas offering late-season water, forcing emergence into upland habitat surrounding these late-season water features and creating a bottleneck of critical upland habitat in terms of protecting sensitive amphibians.

The location of late-season water may not affect amphibians emerging either before local water levels recede or after upland habitat has become saturated with seasonal rains. By late September, Big Lake has completely dried down just as rains begin to saturate upland soils (unpublished manuscript). Ambystomatids prioritize moist locations during dry summer months;

dispersal becomes less selective during months of rain when soil moisture in upland forests is more ubiquitous (Anderson 1967; Pagnucco et al. 2012; Searcy et al. 2013). Salamanders emerging late in the season found dampened soils around most of Big Lake; captures of salamanders in late September and October were not tied to the eastern portion of the lake. Western toads develop within 5-7 weeks and emerge from ponds as early as May at low elevations (Leonard et al. 1993; Wright and Wright 1949). At Big Lake, toads began emerging in mid-June when water still reached most corners of the lake; emergence was tied more to high levels of canopy cover than any one end of the lake. Emerging by mid-July, chorus frogs showed no association with one end of the lake. As late-season dry-down poses a threat to amphibians requiring long hydroperiods (Maxell 2000; Viers et al. 2013), management of fuel treatments over the coming decades should consider protection of upland habitat surrounding these critical areas of late-season water.

Capture rates of all species and life stages decreased with distance to lake; yet results showed a disparity between captures of adult and metamorphic long-toed salamanders as over half of all emergent salamanders were captured 30 m or more from the lake. In higher elevation sites, young long-toed salamanders spend 1-3 years in upland forests before returning to breed as adults (Anderson 1967; Howard and Wallace 1985; Leonard et al. 1993). Young ambystomatids disperse an average of 70 m and may move over 100 m from breeding ponds within their first season (Howard and Wallace 1985; Semlitsch 1998). Our results suggest similar findings and may support evidence that early migrations are motivated to a degree by negative density dependence. Metamorphic salamanders moved farther from the lake during the 'boom' year of 2019 compared to previous years. As young ambystomatids are known to alter their distribution patterns based on density of conspecifics (Regosin et al. 2003; Searcy et al. 2015), crowded

cover objects and foraging grounds during 'boom' years may drive young salamanders at Big

Lake to move farther upland to avoid intraspecific competition.

A high capture rate of adult long-toed salamanders in traps located 3 m from Big Lake

suggests selection for overwintering close to breeding ponds in high elevation locations with

shortened hydroperiods. Captures in proximity to the lake during the fall migration period

suggest adults do not migrate far from Big Lake; rather they overwinter in proximity to the lake

and emerge to breed in spring. After breeding, adult ambystomatids at elevations below 1,000 m

travel an average of 100-150 m and up to 300 m from breeding sites into upland habitat for

overwintering (Beneski et al. 1986; Pilliod and Fronzuto 2005; Semlitsch 1998; Trenham and

Shaffer 2005). Yet adult long-toed salamanders at sites over 1,000 m in elevation have been

detected much closer to breeding ponds (Howard and Wallace 1985, Kezer and Farner 1955).

Our findings correspond with results from Pagnucco et al. (2012) that noted adult long-toed

salamanders overwintered 25-75 m from a breeding pond at an elevation of 1,290 m in Alberta,

Canada. First arrival at breeding ponds is often paramount to successful breeding for pond-

breeding amphibians (Beneski et al. 1986; Verrell and Pelton 1996) and may be of particular

importance for species with long larval development times. Requiring a minimum of 10 weeks

for larval development, long-toed salamanders may experience strong selection pressures for first

arrival and early breeding at high elevation sites that experience a shortened hydroperiod as a

result of lingering ice cover. Migrations away from the lake in the fall may be more difficult to

repeat in the spring when the ground is snow covered; adults at Big Lake may choose to

overwinter in burrows close to the lake to be available for spring breeding.

Debris Piles

Despite high amphibian surface activity during the week of debris pile surveys, evidence that amphibians used newly formed debris piles was absent. Percent woody debris cover increased in treatment plots, most likely a result of debris additions from treatments. Yet after treatments, the quality of debris as cover for amphibians most likely decreased as select existing woody debris was gathered into piles. Amphibians often select cover objects showing moderate levels of decay as these logs and stumps provide increased moisture and microhabitat opportunities over freshly fallen debris (Pilliod et al. 2006; Welsh and Hodgson 2008). Though debris piles may conserve soil moisture during dry summer months, the debris piles at Big Lake did not appear to offer increased soil moisture levels in October when surrounding soils were cool and wet (pers. obs.). The ground beneath debris piles also revealed a layer of pine needles several inches thick that may present amphibians with a physical obstacle and an increase in soil acidity. Following fuel treatments, most debris piles are left for 1-2 seasons for wood to dry (Bishop and Haas 2005; Garman et al. 2001) and are burned outside of peak fire season (in fall or winter) when conditions are wet and fires may be controlled (Bishop and Haas 2005; Hossack and Pilliod 2011). The debris piles at Big Lake are scheduled to be burned in the fall of 2020. A year of settling and decaying may make these logs more desirable cover objects for amphibians, making debris piles a potential hazard to individuals seeking cover prior to burning. Future research should emphasize the degree to which amphibians use debris piles as cover in the seasons immediately following fuel treatments.

Management Implications

Understory thinning treatments implemented via hand-thinning and piling methods may show no short-term impacts to the abundance or survival of pond-breeding amphibians within coniferous forests. While mechanical thinning often results in ground disturbance that affects microhabitat conditions for amphibians, hand-thinning methods at Big Lake were able to avoid such disturbance and may be useful in particularly sensitive aquatic-adjacent habitat. As decreases in tree density may lead to long-term soil erosion and loss of leaf litter inputs, future considerations should include long-term assessments of litter and soil integrity in aquatic-adjacent habitat beyond the first year following thinning.

Some aquatic-dependent species may benefit from the thinning of overgrown pine stands near breeding ponds if implementation avoids substantial ground disturbance. Upland habitat associations often occur on a species-specific level based on life history needs; management decisions should consider separately the biology of each aquatic-dependent species. The specific hydrology of ephemeral wetlands should be considered by forest managers as upland habitat surrounding the location of late-season water may require special protection. Our results also suggest adult amphibians threatened by shortened hydroperiods may overwinter close to breeding ponds to facilitate early breeding in spring. More research is needed to assess migration patterns of adult long-toed salamanders at high elevations.

The burning of debris piles following thinning treatments may be a concern for local amphibians, especially when treatments include the piling of existing woody debris. Although no amphibians were found using debris piles as cover in our study, these piles will have another year to settle and decay, becoming appealing cover objects to amphibians in an area where

existing decayed logs were removed during treatments. Such debris piles should be surveyed for amphibians in the weeks leading up to burning.

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Table 1: Results of GLMMs evaluating the effect of thinning on amphibian captures. This table displays the results of the generalized linear mixed models with trap-level amphibian captures as the response variable for long-toed salamanders (AMMA), western toads (ANBO), and Pacific chorus frogs (PSRE). Results are listed for each of the three predictor variables of interest for each species and life stage including treatment and the interaction terms between treatment and 'distance to late-season water' and 'distance to lake.'

Species + Life Stage	Predictor Variable	Estimate	X^2	D.f.	P-value
AMMA Adult	Treatment	-0.031	0.03	1	0.87
	Treatment*Distance to late-season water	0.001	0.4	1	0.53
	Treatment*Distance to lake	0.008	1.15	1	0.28
AMMA Young	Treatment	-0.018	0.03	1	0.87
	Treatment*Distance to late-season water	-0.001	1.3	1	0.25
	Treatment*Distance to lake	-0.002	0.12	1	0.73
ANBO Young	Treatment	0.004	0	1	0.99
	Treatment*Distance to late-season water	-0.003	1.42	1	0.23
	Treatment*Distance to lake	0.011	1.51	1	0.22
PSRE Young	Treatment	0.386	3.04	1	0.08
	Treatment*Distance to late-season water	-0.011	1	1	0.32
	Treatment*Distance to lake	-0.001	2.81	1	0.09

Table 2: Results of GLMMs evaluating associations between habitat variables and amphibian captures. This table displays results of the generalized linear mixed models with a response variable of trap-level amphibian captures summarized at the survey level. Results are listed for each of the seven predictor variables for each species and life stage and include tree density, canopy cover, leaf litter depth, woody debris cover, the trap's distance to lake, slope, and the trap's distance to late-season water. Model selection removed the variable 'distance to late-season water' from the models for salamander adults, salamander young with no emergence (captured after 20 Sept.), and Pacific chorus frogs. P-values were generated from likelihood ratio tests; confidence intervals refer to incidence rate ratios. Species codes are as follows: long-toed salamanders (AMMA), western toads (ANBO), and Pacific chorus frogs (PSRE).

Variable	AMMA Adults			AMMA Young			AMMA Young (No Emergence)			ANBO Young			PSRE Young		
	Incidence Rate Ratios	Confidence Intervals	P-value	Incidence Rate Ratios	Confidence Intervals	P-value	Incidence Rate Ratios	Confidence Intervals	P-value	Incidence Rate Ratios	Confidence Intervals	P-value	Incidence Rate Ratios	Confidence Intervals	P-value
Tree density	0.81	0.69-0.94	0.01	0.87	0.76-0.99	0.03	0.76	0.63-0.92	0.005	1.05	0.84-1.32	0.66	0.72	0.60-0.85	<0.001
Canopy cover	1.29	1.11-1.49	0.001	0.98	0.87-1.10	0.68	1.03	0.85-1.25	0.76	1.48	1.14-1.92	0.003	0.92	0.78-1.08	0.30
Leaf litter depth	1.15	1.03-1.29	0.01	1.03	0.92-1.16	0.60	1.09	0.92-1.30	0.32	0.81	0.64-1.02	0.08	1.2	1.05-1.38	0.009
Woody debris cover	0.85	0.74-0.98	0.02	0.88	0.79-0.97	0.01	0.92	0.78-1.08	0.29	0.91	0.73-1.12	0.37	0.81	0.70-0.93	0.003
Distance to lake	0.55	0.47-0.64	<0.001	0.88	0.77-0.99	0.04	0.82	0.68-0.99	0.04	0.68	0.53-0.88	0.004	0.76	0.64-0.90	0.001
Slope	0.94	0.81-1.09	0.41	1.09	0.98-1.20	0.11	1.15	0.97-1.35	0.10	0.93	0.75-1.14	0.46	0.94	0.82-1.07	0.33
Distance to late-season water	N/A	N/A	N/A	0.58	0.52-0.65	<0.001	N/A	N/A	N/A	1.32	1.07-1.64	0.01	N/A	N/A	N/A

Table 3: Summary statistics of variables included in GLLMs evaluating associations between habitat variables and long-toed salamander captures. Each of the seven predictor variables used in the habitat analysis are listed ('Variable Name') along with the corresponding units used. The column 'Group' refers to the habitat category into which each habitat variable was grouped for model selection purposes. Summary statistics for each variable are listed based on the results of vegetation surveys and include the mean, range and standard deviation ('SD') of all survey results for each variable.

Group	Variable Name	Units	Mean	Range	SD
Late-season water	Distance to late-season water	Meters	331	25 - 674	193
Forest	Tree density	Trees/m^2	48.9	5.3 - 160.0	38.2
Forest	Canopy cover	% cover	76.9	54.7 - 95.7	11.3
Soil	Leaf litter depth	Cm	7.9	3.7 - 13.7	2.0
Soil	Woody debris cover	% cover	27.7	9.8 - 53.8	11.2
Geometry	Distance to lake	Meters	29.4	3.0 - 114.0	23.6
Geometry	Slope	Degrees	-3.6	-9.0 - -1.5	2.1

Figure 1: Map of treatment and control plots and pitfall trap locations at Big Lake. The map shows Big Lake, the layout of the 14 control and 12 treatment plots and the location of all 78 pitfall traps from the 2018 and 2019 seasons (2017 locations not shown). Also labeled are the location of the lake's main spring and outflow as well as the location of late-season water. Map details provided by Becky Howard.
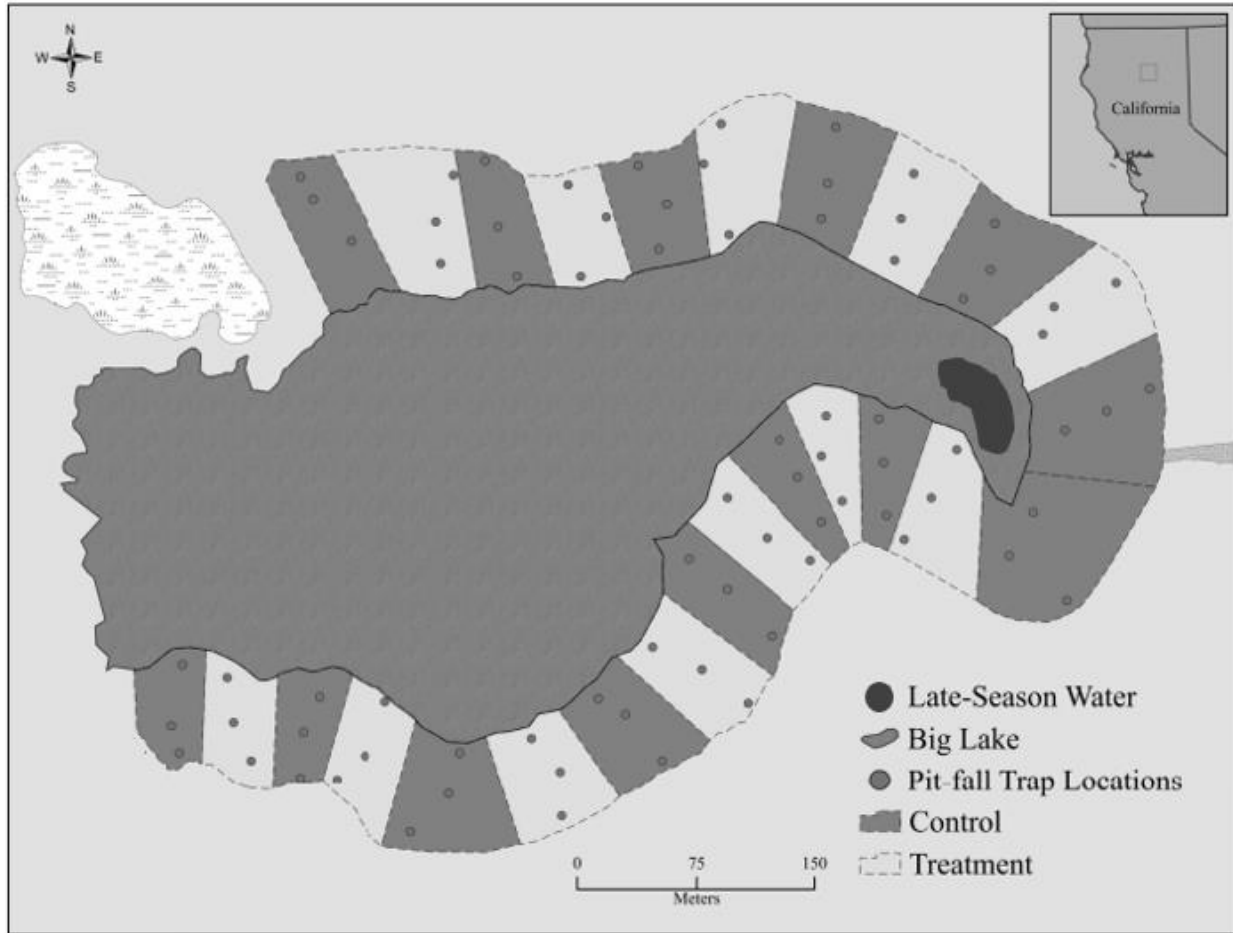
Figure 2: Treatment plots before/after treatments with debris piles and the location of late-season water.
Shown below are images of a treatment plot before (panel A) and after (panel B) treatment, as well as a woody debris pile collected after treatment implementation (panel C) and the location of late-season water with upland forest habitat in the background (panel D).
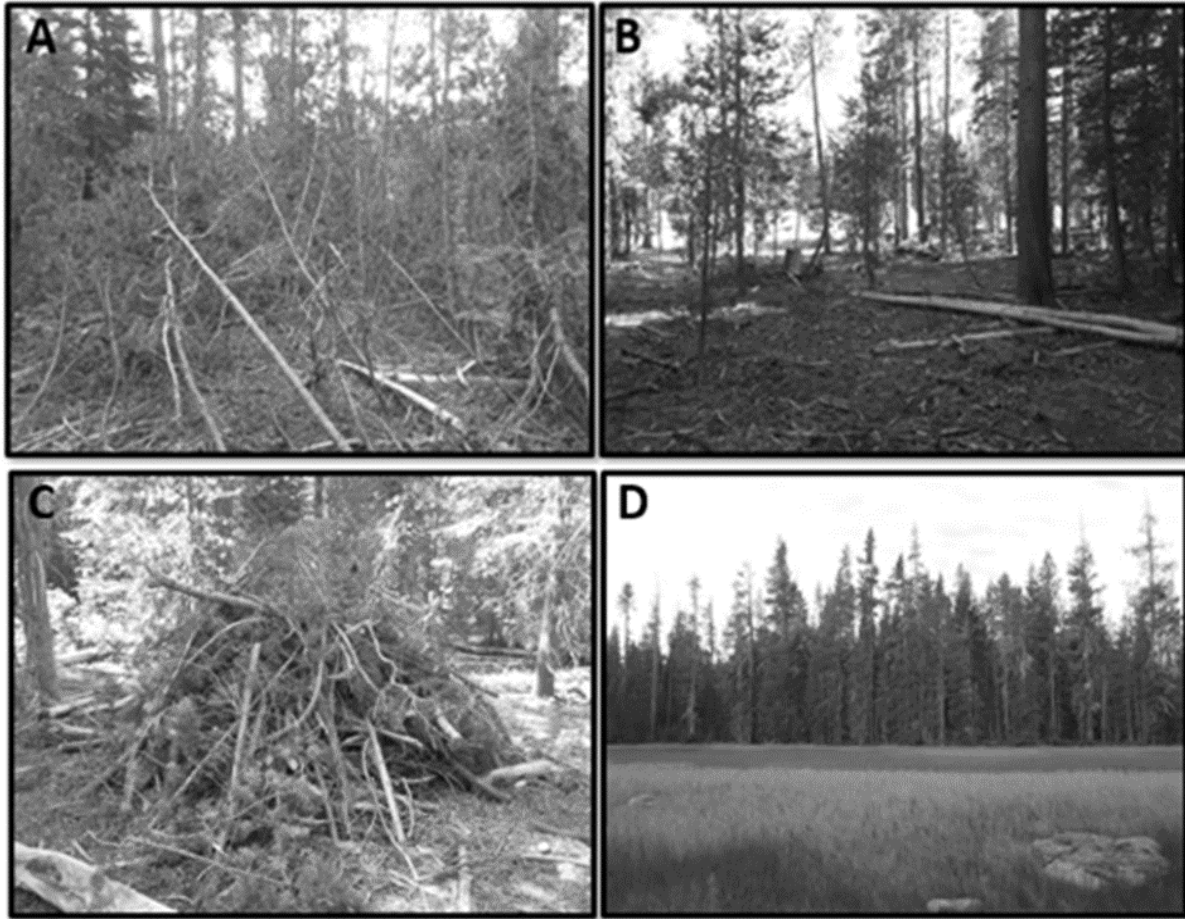
Figure 3: Effect of thinning treatments on upland habitat conditions. The means and standard errors of post treatment habitat measurements are shown by treatment type. Values were calculated based on plot-level averages of 5 m radius vegetation surveys conducted post treatment (2019). Units vary for each habitat variable and include canopy cover (% cover), leaf litter depth (depth in centimeters), tree density (trees/m^2), and woody debris cover (% ground cover).
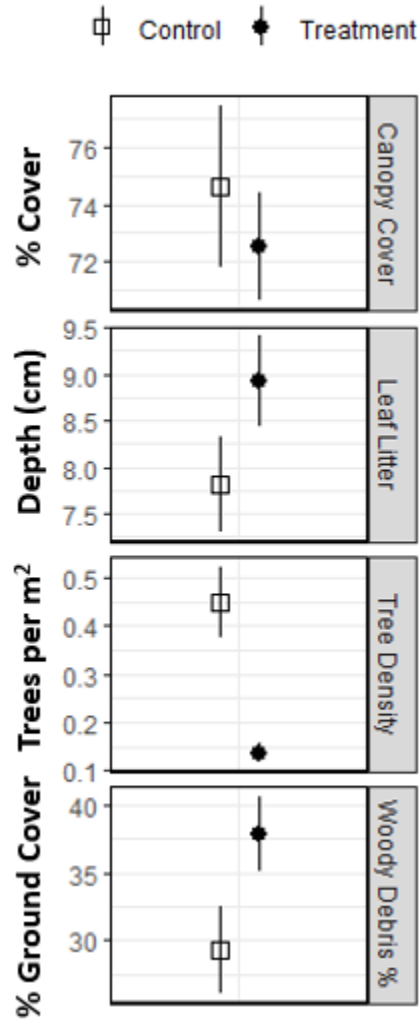
Figure 4: Effect of thinning on amphibian movement. Post treatment (2019) capture rates are shown with standard errors for adult and newly metamorphosed long-toed salamanders (AMMA), metamorphic western toads (ANBO) and metamorphic Pacific chorus frogs (PSRE). Capture rates were calculated based on total captures in each trap divided by the number of trap-days and are separated by treatment type.
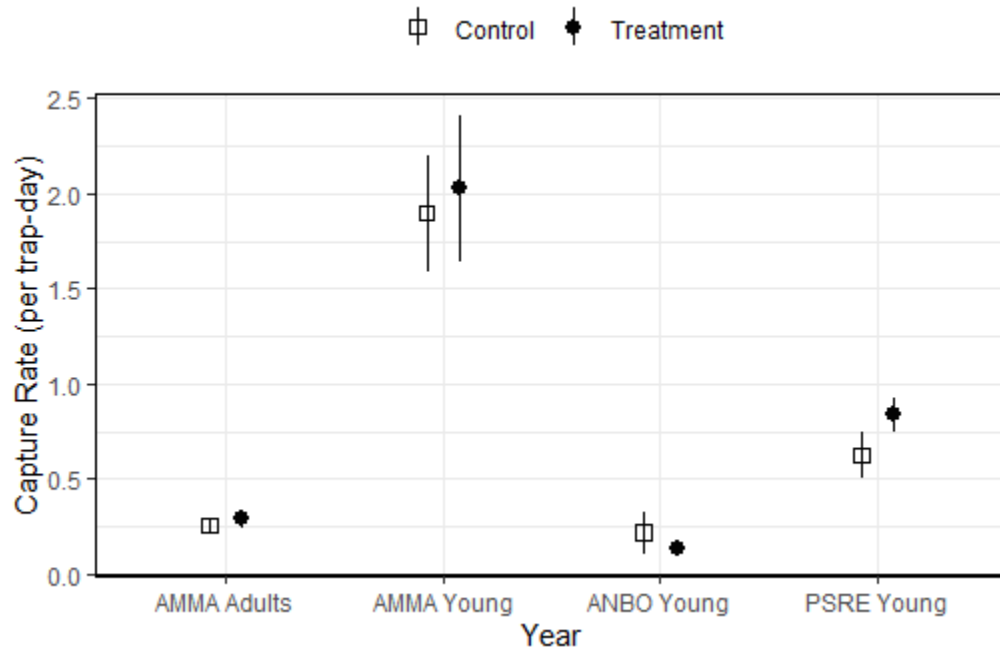
APPENDIX

A: Summary of dates, trap availability, and amphibian captures for each survey trip to Big Lake in 2019. Summary data is listed for each post treatment survey trip to Big Lake that was used in treatment analyses (captures from spring and early summer survey trips were removed from analysis). Included for each survey trip ('Survey Code') is the corresponding year, dates and number of days for each survey trip. The '% Days Unavail' column indicates the percentage of traps that were not available during that survey as a result of treatment implementation or damaged traps. The final four columns list the total number of captures of each species and life stage used in analysis during this survey, which was used as the response variable in the habitat analysis. Species codes are as follows: long-toed salamanders (AMMA), western toads (ANBO), and Pacific chorus frogs (PSRE).

Survey Code	Year	Dates	No. Days	% Days Unavail.	AMMA Adults	AMMA Young	ANBO Young	PSRE Young
19.1	2019	8 Aug – 22 Aug	15	10.4	15	701	521	1,367
19.2	2019	27 Aug – 30 Aug	4	10.3	0	220	32	124
19.3	2019	7 Sep – 12 Sep	6	6.9	0	909	52	335
19.4	2019	17 Sep – 19 Sep	3	0.07	35	2,028	104	459
19.5	2019	28 Sep – 29 Sep	2	0.7	155	45	30	34
19.6	2019	17 Oct – 21 Oct	5	0.2	280	137	15	194

B: Summary of model weights and top models used for habitat analysis. The top performing models for each species and life stage combinations were selected via AIC. Model weights are listed for each of the five species and life stages, including long-toed salamander (AMMA) adults, young and young with no emergence (captured after 20 September), western toads (ANBO), and Pacific chorus frogs (PSRE). The highest model weights for each species and life stage were used for hypothesis testing and are shown in bold. The individual habitat variables included in each model are listed in the column 'Habitat Variables Included' while the column 'Habitat Categories Used' indicates the four habitat categories used as the unit of adding or dropping variables in model selection and are named as follows: 1) late-season water, 2) forest (tree density, canopy cover), 3) soil (leaf litter depth, woody debris cover), and 4) geometry (distance to lake, slope). Model combinations with all five model weights <0.01 were not included in the table.

Habitat Categories Used	Habitat Variables Included	AMMA Adults	AMMA Young	AMMA Young (No Emerg.)	ANBO Young	PSRE Young
Forest, geometry, late-season water, soil	Distance to late-season water, tree density, canopy cover, leaf litter depth, woody debris cover, distance to lake, slope	0.38	**0.7**	0.37	**0.86**	0.27
Forest, geometry, soil	Tree density, canopy cover, leaf litter depth, woody debris cover, distance to lake, slope	**0.59**	0	**0.39**	0.1	**0.73**
Geometry, late-season water, soil	Distance to late-season water, leaf litter depth, woody debris cover, distance to lake, slope	0	0.29	0.12	0.03	0
Forest, geometry	Tree density, canopy cover, distance to lake, slope	0.02	0	0.03	0	0
Geometry, soil	Leaf litter depth, woody debris cover, distance to lake, slope	0.01	0	0.04	0	0
Forest, geometry, late-season water	Distance to late-season water, tree density, canopy cover, distance to lake, slope	0.01	0.01	0.02	0	0
Geometry, late-season water	Distance to late-season water, distance to lake, slope	0	0.01	0.02	0	0
Geometry	Distance to lake, slope	0	0	0.01	0	0