Ecology of the Cascades Frog (*Rana cascadae)* and Interactions with Garter Snakes and Nonnative Trout in the Trinity Alps Wilderness, California

By:

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December 2007

Final Report To:

California Department of Fish and Game
Habitat Conservation Planning Branch
1416 Ninth Street, Suite 1280
Sacramento, CA 95814

and

National Fish and Wildlife Foundation
Bring Back The Natives Grant Program
1120 Connecticut Avenue NW, Suite 900
Washington, DC 20036

Cover Photos: Adult female Cascades frog (*Rana cascadae*), aquatic garter snake (*Thamnophis atratus*) captured in Echo Lake basin regurgitating an Eastern brook trout (*Salvelinus fontinalis*), surveying Atlantis meadows west of Red Mountain summit, Trinity Alps Wilderness, California. (*Photos: J. Garwood*)

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FINAL REPORT TO THE CALIFORNIA DEPARTMENT OF FISH AND GAME AND NATIONAL FISH AND WILDLIFE FOUNDATION

DFG CONTRACT NO. P0385107

NFWF CONTRACT NO. 2004-0075-000, Bring Back The Natives Grant

Administered By: Humboldt State University Sponsored Programs Foundation
P.O. Box 1185
Arcata, CA 95518-1185

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ECOLOGY OF THE CASCADES FROG (*RANA CASCADAE*) AND INTERACTIONS WITH GARTER SNAKES AND NONNATIVE TROUT IN THE TRINITY ALPS WILDERNESS, CALIFORNIA [1/]

December, 2007

By

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[1/] Final Report for the California Department of Fish and Game Contract No. P0385107 and National Fish and Wildlife Foundation Contract No. 2004-0075-000

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Report Citation:

Garwood, J.M., and Welsh, H.H. Jr. 2007. Ecology of the Cascades frog (*Rana cascadae*) and interactions with garter snakes and nonnative trout in the Trinity Alps Wilderness, California. Final report prepared for the California Department of Fish and Game and the National Fish and Wildlife Foundation. Arcata, CA 87pp.

ABSTRACT

This study combined both intensive and long-term sampling components at multiple spatial scales to provide information on Cascades frog (*Rana cascadae*) ecology in the Trinity Alps Wilderness of Northern California. We used mark-recapture and radio telemetry from 2003 to 2007 to determine key ecological components of Cascades frog life history, habitat use, spatial patterns, migrations and dispersal for all age classes. We found Cascades frogs used a variety of habitats for breeding, summer foraging and over-wintering, but it was common for these habitats to be spatially or temporally separated and frogs were observed to move seasonally among them. Migrations and dispersal events were common among isolated habitats indicating that, in many cases, single sites are not likely to be self-sustaining, but contribute to a matrix of required resources across a patchy landscape. Furthermore, based on extensive migrations and dispersal we found the population dynamics of Cascades frogs to be operating across a whole-basin, so conservation of this species will require making decisions that reflect this scale.

We also studied the role of Cascades frogs in local food web dynamics, including their relationships with both natural and introduced predators. This included two native garter snakes (*Thamnophis* spp.) and introduced trout. We used mark-recapture and collected non-lethal diet samples on both garter snake species during regular visual encounter surveys to determine the density, diet, distribution and movement patterns of each species. We also determined distribution and density of introduced trout at a basin-wide scale. Our results indicate one species of garter snake (*T. atratus*) was found to occur in high densities in areas with trout, and has adopted eating introduced trout as a subsidized food source. This species also feeds on amphibians. Conversely, the other garter snake species (*T. sirtalis*) foraged exclusively on amphibians and had lower overall densities across the landscape. These observations suggest introduced trout could be impacting native amphibians indirectly through altered food-web dynamics. The results from this study fill important knowledge gaps with regard to the life history of the Cascades frog, and its role in a community with both native and introduced predators. We provide recommendations to assist stakeholders in designing management strategies more tailored to the ecological requirements of Cascades frogs which will benefit future generations of this declining amphibian.

ACKNOWLEDGEMENTS

This investigation, including all information provided in this report, is the result of a collaboration between the California Department of Fish and Game (DFG), the National Fish and Wildlife Foundation, Humboldt State University Sponsored Programs Foundation, The US forest Service, Pacific Southwest Research Station, Redwood Sciences Laboratory, The World Conservation Union, Amphibian Specialist Group (Formally the Declining Amphibian Populations Task Force) and the USGS Amphibian Research and Monitoring Initiative. This large collaboration could not have succeeded without the support and initiation of matching funds provided by DFG; we sincerely thank Betsy Bolster for her pivotal role in establishing and managing this contract professionally from start to finish. We also kindly thank Terry Roelofs at Humboldt State University for helping establish these contracts. We are in debt to Clara Wheeler, Ryan Bourque, and Monty Larson for their substantial assistance and expertise with data collection and study design as well as general support throughout this project. They are all exceptional ecologists and preformed beyond our expectations. Other individuals contributed their weekends or vacations to assist in this project including: Terra Fuller, Nate Nieto, James Bettaso, Laura Burkholder, Rebecca Studebaker, Joshua Dorris, William Wheeler, Abby Wheeler, Kara Cox, Jacob Ehlerding, Molly Alles, Jon Stead, Karen Pope, Cheryl Bondi, Betsy Bolster, Cara McGary, Erin Hannelly, Brian Jennings, Cain Adams, and Reuben Koontz. We thank Lorna and Paul Garwood for providing the unofficial base camp and catering service, especially after long trips in the mountains. Becky Howard provided invaluable database assistance. Jim Hotchkiss and Eric Haney from DFG provided essential GPS equipment and thorough training for accurate mapping and spatial data collection. We also thank Bernard Aguilar from DFG for providing backpacking equipment and general support of this study throughout. Garth Hodgson, Karen Pope, Don Ashton, Clara Wheeler, Luke George, and Matthew Johnson provided expert knowledge and discussion on analysis. Rebecca Studebaker, Clara Wheeler, and Karen Pope improved sections of this report. This research was in cooperation with Humboldt State University Sponsored Programs Foundation which received and managed three external grants: California Department of Fish and Game contract agreement #P0385107; National Fish and Wildlife Foundation grant: Cascades frog Ecology and Management #2004-0075-000; and the Declining Amphibian Populations Task Force graduate seed grant to JMG. We thank Julie Davy especially for her expertise in setting up and managing these contracts.

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INTRODUCTION

The global decline of amphibians has become a concern over the last two decades with the ranid frogs of western North America among the most seriously impacted of all species. In light of investigations documenting rapid declines of Cascades frogs (*Rana cascadae*) in California (Fellers and Drost 1993, Jennings and Hayes 1994, Davidson et al. 2002, Welsh et al. 2006, Fellers et al. 2008) renewed attention has been placed on the conservation of this species. One central problem regarding the management of Cascades frog populations in California is the lack of information on general life history requirements of the species, as well as its role in the ecological community. Understanding a species' natural history is essential for successful conservation and management of the species (Bury 2006). Although a number of published studies have concentrated on various aspects of Cascades frog ecology and reasons for declines, (see Jennings and Hayes (1994), Pearl and Adams (2005), and Fellers et al. (2008) for a review), considerable knowledge gaps remain regarding the general ecology of the Cascades frog in California.

Most studies relevant to Cascades frog ecology have been concentrated in the northern portions of their range including Oregon and Washington. Recent genetic work by Monsen and Blouin (2003) revealed substantial divergence in the genome of Cascades frogs populations in California compared to those found Oregon and Washington. This work suggests California populations have been separated from Oregon and Washington since the beginning of the last glacial maximum (approximately 2mya) and recognize California populations as a distinct population segment (DSP). Populations of Cascades frogs in Oregon and Washington may also differ from California populations because they occupy landscapes that are likely different (both physically and biologically) than those within California. Based on genetic and potential landscape differences, populations on regional scales can have distinctly different habitat associations, phenologies, and roles in the community.

The focus of many studies previously conducted on Cascades frogs centered on reproduction, including various environmental factors affecting egg and larvae occurrence and survival. Studies focusing on reproduction are valuable, however understanding the full compliment of a species life history depends on a thorough investigation over its entire annual activity period while accounting for specific demographic parameters such as age and sex. Recent studies on other anurans elucidate this point, indicating many species have the tendency to use multiple resources annually (Sinsch 1990, Pope et al. 2000, Pope and Matthews 2001, Pilliod 2002). These resources are often spatially separated within a patchy landscape, so single site investigations lack demographic independence (Petranka et al. 2004). All of the previous detailed life history information on Cascades frogs is largely limited to single isolated habitats. For example, the only study on Cascades frog population dynamics occurred at one small isolated pond in the Oregon Cascades Range (Briggs and Storm 1970). Although valuable, insights from studies at isolated sites cannot be used to manage populations occupying patchily distributed habitats in close proximity (< 1km apart).

Many previous studies on Cascades frogs have focused on large-scale, short term distributional relationships of the species in Oregon and Washington (Brown 1997, Bury and Major 1997), as well as California (Fellers and Drost 1993, Fellers 1998, Koo et al. 2004, Stead et al. 2005, Welsh et al. 2006, Stead and Pope 2007). These studies were conducted using snapshot visual encounter surveys with an emphasis on regional distributions and large-scale habitat associations. Although these efforts have been crucial for identifying gross habitat associations and timely regional distributions, they provide no information on temporal use of habitats by different age classes of Cascades frogs at scales relevant to the populations as a whole.

The significance Cascades frogs have on local food web dynamics has been overlooked with no information available beyond brief observational notes. Studies on other anuran species emphasize the role frogs have in community structure, both as predators (Bull 2003, Finlay and Vredenburg 2007) and prey (Kephart 1982, Gregory and Isaac 2004, Matthews et al. 2002). Understanding the role Cascades frogs have in food web dynamics is an essential component to their conservation. In this study we focused on native and introduced predators of Cascades frogs. Other ongoing studies in California are also defining specific roles Cascades frogs have in the community; these include a detailed experimental field study by Karen Pope (*USFS/ UC Davis*) and a diet study on Cascades frogs by Monty Larson (*USFS/ Humboldt State University*).

This study provides a much needed detailed ecological study on Cascades frogs in California. The primary objectives of this project were to determine key aspects of Cascades frog life history at a population scale, as well as to determine its role in a community with both native and non-native predators. We specifically focused on age-based seasonal habitat use, movement patterns, and reproductive ecology of an entire population of Cascades frogs. In addition, we studied the role Cascades frogs have in local food web dynamics including novel associations with non-native brook trout.

Species Descriptions and Backgrounds

Cascades Frog

The Cascades frog was first identified as a unique species among the western ranid frog complex by Slater (1939). Cascades frogs can be identified from other western ranids by well-defined, inky black dorsal spots and a yellow upper jaw stripe that extends almost to the shoulder (Olson 2005) (Figure 1). The Cascades frog is considered to be medium sized among western ranid frogs. In this study, we found females up to 81 mm snout-urostyle length (SUL) and weighing as much as 56 g when gravid. Males grew up to 67 mm SUL and weighed as much as 28g.

Figure 1. Photographs of three Cascades frogs (*Rana cascadae*) captured in Upper Deep Creek basin, Trinity Alps Wilderness, California. Left individual is a juvenile, middle individual was an adult male (*Photo credit: Jamie Bettaso*), right individual was a gravid adult female.

Cascades frogs range from the northern Sierra Nevada Mountains, north throughout the Cascades Ranges of California, Oregon, and Washington. Two isolated populations occur west of the Sierra Nevada/Cascade range in the Olympic Peninsula in Washington and the Klamath mountains in Northern California. In California, Cascades frog distribution is associated with montane and sub-alpine landscapes. Known extant California populations appear to be restricted to elevations above 1220 m (Welsh et. al 2006, Stead and Pope 2007, J. Garwood pers. obs.). This creates a highly fragmented "island" distribution for this species in Northern California. In the Klamath Mountains, where this study took place, the majority of the Cascades frogs distribution is within 779,400 acres of protected lands, which include the Trinity Alps, Russian, and Marble Mountain Wilderness areas (Welsh et al. 2006). Disjunct populations of Cascades frogs in the Klamath Province are also distributed throughout Mount Eddy and both slopes of the Shasta-Trinity Divide. In the Shasta/Lassen region, small remnant populations of Cascades frogs appear to be extremely isolated from one another (Fellers et al. 2008).

Across their range, Cascades frogs reproduce once annually, immediately after surface waters begin to thaw (Sype 1975, Briggs 1976, Nussbaum et al. 1983, *this study*). Egg masses containing 300-500 ova are typically oviposited on shallow benches or alcoves of lentic water-bodies (Briggs 1976, Nussbaum et al. 1983, *this study*). Although unobserved during hundreds of site visits in the Klamath Mountains, Cascades frog egg masses were discovered in slow flowing meadow streams at three locations within the Lassen region in 2007 (J. Garwood, pers. obs.). Cascades frogs have a single year larval development period, with tadpoles metamorphosing into frogs by late summer (Sype 1975, Nussbaum et al. 1983, Briggs 1987, *this study*). This is unlike the Mountain and Sierra Yellow-Legged frogs (*R. muscosa* and *R. sierra*) which are closely related species that retain larval stages for up to three years (Vredenburg et al. 2005). Although individual movement patterns of adult Cascades frogs are poorly known, adults and juveniles have previously been documented using a wider variety of habitats than those used for breeding. Bury and Major (1997) (*in Washington*), Brown (1997) (*in Oregon*) and Welsh et al. (2006) (*in California*) observed Cascades frogs in all types of aquatic habitats including ponds, meadows, deep lakes, and creeks. These observations demonstrate Cascades frogs use a variety of habitats and suggests individuals may move seasonally depending on specific life history attributes such as breeding, summer and wintering.

The Cascades frog has been listed as a California species of special concern since 1994 (Jennings and Hayes 1994) and has been considered "sensitive" throughout USDA Forest Service Region 5 since 1998 (USDA Forest Service). The Cascades frog is also listed as "near threatened" on the global IUCN Red List in 2007 (www.iucnredlist.org).

Garter Snakes

The region has two species of garter snakes: the common garter snake (*Thamnophis sirtalis*) and the Pacific coast aquatic garter snake (*Thamnophis atratus hydrophilus*) (hereafter aquatic garter snake). The common garter snake has been described as the most successful reptile species in North America and is the most widespread of all reptiles in the region (Rossman et al. 1996, St. John 2002). The aquatic garter snake has a much narrower distribution, occurring in northwestern California and southwestern Oregon (St. John 2002), where it is considered to be closely tied to stream habitats (St. John 2002, Lind et al. 2005). Based on existing literature for Northern California, both species are dependent on aquatic prey. Common garter snakes regionally prey primarily on amphibians (Kephart 1982, Rossman et al. 1996), whereas aquatic garter snakes prey on both amphibians and fish (Lind and Welsh 1994), using uniquely derived foraging techniques (Welsh and Lind 2000). Similar to the high Sierra Nevada, we consider garter snakes in the montane to sub-alpine Klamath Bioregion to be the top native predator in these aquatic ecosystems (see: Jennings et al. 1992, Matthews et al. 2002).

Introduced Brook Trout

Brook trout (*Salvelinus fontinalis*)* are native to Eastern North America, though they are the most widely stocked trout in high mountain lakes of the Western United States (Bahls 1992), especially in Northern California (Welsh et al. 2006). Brook trout are especially adapted to montane and sub-alpine environments and are among the most cold tolerant of salmonids, having the ability to reproduce in lakes, and reaching reproductive maturity at a young age (Moyle 2002). These life history traits make brook trout particularly successful in high-elevation lakes with populations persisting years after stocking has ceased (Bahls 1992, Knapp 1996). Established brook trout populations in headwater lakes have also allowed this species to invade stream networks associated with these lakes, increasing their overall distributions beyond managed portions of these watersheds (Adams et al. 2001, Welsh et al. 2006, J. Garwood, pers. obs.). Brook trout are considered opportunistic predators, feeding on a variety of available invertebrates (Moyle 2002) as well as palatable amphibians (Resetarits 1991, Bradford 1989, Vredenberg 2004, Welsh et al. 2006).

**Technically a char because they are members of the genus Salvelinus. Based on current and historic naming, we will refer to them here as trout.*

SITE DESCRIPTION AND BACKGROUND

Study Area Description

This study was conducted within the headwaters of Deep Creek, located at the southeastern portion of the Trinity Alps Wilderness, Klamath Province, California (UTM, NAD27 CONUS; 509208E, 4530371N) (Figure 2). The entire watershed is west facing and drains into the Stuart's Fork, a major tributary of the upper Trinity River. The upper portion of Deep Creek, where the study took place, is a medium sized glacial cirque basin (601 ha) encompassed by steep jagged peaks reaching elevations up to 2497 m, which are among some of the highest in the Klamath Province. The basin is further dissected into two smaller sub-basins (hereafter Echo Lake and Siligo basins) of similar size by a west trending jagged arête (Figure 2). The geology of the study area is dominated by the serpentine rich Trinity ultramafic pluton which is thought to have formed in the late Jurassic period (Lipman 1964). Other rocks present in lesser amounts include various small granite intrusions, gabbro, and schist's. The majority of the basins' topography consists of steep elevational gradients composed of bare rock outcrops and expansive talus fields. Upper Deep Creek has been further characterized by periodic glaciation, thought most recently from two separate events within the Pleistocene epoch (Sharp 1960). As a result, superficial glacial deposits and moraines are scattered throughout the area, adding to the complex topography. This terrain is typical when compared to other basins in this isolated and rugged region.

The flora of the Trinity Alps has been described in detail by Ferlatte (1974). Floristic zones well represented in Deep Creek basin include open sub-alpine forest, montane chaparral, and sub-alpine meadow which are composed of serpentine tolerant plant species. Thin patches of

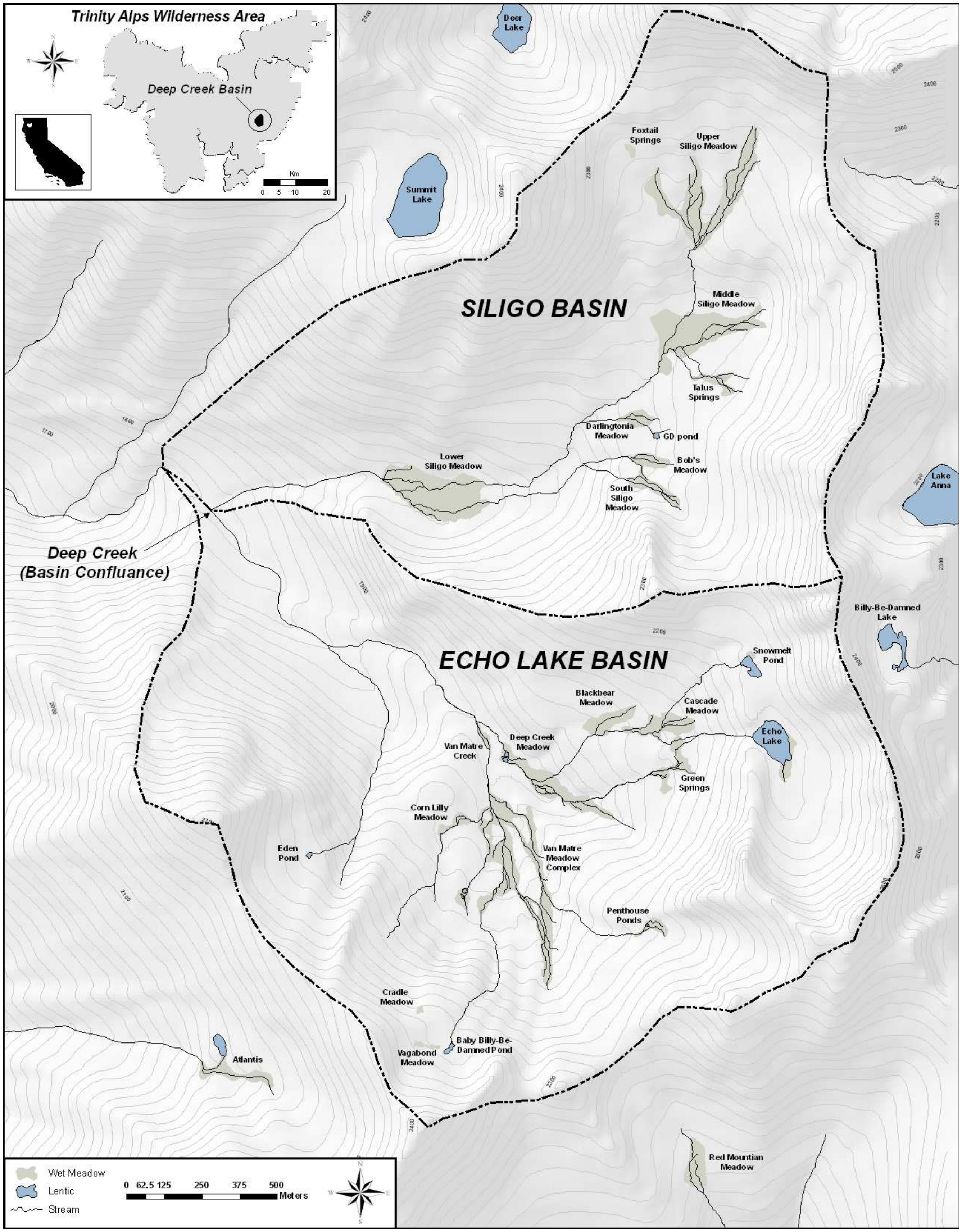


Figure 2. Map of survey sites within, and proximal to, the Upper Deep Creek drainage located in the southeast Trinity Alps Wilderness, California. Black hatch lines represent catchment boundaries for both Echo Lake and Siligo sub-basins. Major elevation contours represent 100 meter intervals.

western white pine (*Pinus monticola*), foxtail pine (*P. balfouriana*) and jeffrey pine (*P. jeffreyi*) dominate the sparse forest canopy, which contains a total of six conifer species overall. Huckleberry oak (*Quercus vaccinifolia*), angelica (*Angelica arguta*) dominate dry exposed slopes of montane chaparral. Meadow patches contain a variety flowering plants, but are dominated by sedges (*Cyperaceae*) and grasses (*Poaceae*), along with corn lily (*Veratrum californicum*), white-flowered schoenolirion (*Schoenolirion album*), California pitcher plant (*Darlingtonia californica*), meadow goldenrod (*Solidago canadensis elongata*), and mountain spiraea (*Spiraea densiflora*).

The climate of the Klamath Mountains is mediterranean, characterized by wet, cool winters and dry, warm summers. However, the local expression of this climate regime is remarkably variable due to a strong west to east moisture and temperature gradient caused by proximity to the Pacific Ocean. Steep elevational gradients further this influence on temperature and the spatial pattern of precipitation, through orographic effects (Skinner et al. 2006). During this study, when Cascades frogs were active (May to October), air temperatures ranged from -11.1 to 31.6º C (mean: 12.7º C) at the nearest weather station (Red Rock Mountain, Elevation: 2042 m). In contrast, air temperatures when frogs were over-wintering (November to May) were much cooler ranging from -19.4 to 24.4º C (mean: 0.9º C).

The dominant source of precipitation from November through May falls as snow with the May 1 average equaling 210 cm (CCSS 2007). From 2003 to 2007, regional snow pack was 170%, 125%, 120%, 251%, and 38% respectively of the May 1 average (California Department of Water Resources, online reports: http://cdec.water.ca.gov). Precipitation during the active period of Cascades frogs usually falls as rain. Rainfall events during these months occur largely in the form of isolated thunder storms and are usually sparse. During this study, total rainfall from June through October ranged from 0.4 to 5.5 cm (mean: 2.6 cm) annually.

Although some large ponds and one lake are present in Upper Deep Creek, aquatic features are dominated by sub-alpine wet meadow complexes (Figure 2). These fragile meadows collectively contain hundreds of small ponds and stream segments along with scattered Darlingtonia fens. We limited our study to quantify habitats in Echo Lake basin since the majority of work was concentrated there, but see Figure 2 for a map of aquatic features proximal to Echo Lake basin. The aquatic features in Echo Lake basin include twelve meadows, two large semi-permanent ponds (SMP and EDN), and Echo lake, a medium-sized tarn. During each spring, Echo Lake basin contains an estimated 3.12 hectares of surface water including: one lake, 588 ponds and 13.9 km of streams. These aquatic features range in elevations from 1960 to 2279 m and are located on slopes ranging from 0-48% (mean: 15.5%). Collectively, these features create a matrix of patchy "island" aquatic habitats throughout the basin (Figures 3 and 4). In total, these habitats account for 3.5% of the area in the basin and are surrounded by inhospitable dry rocky slopes, steep talus fields and post-glacial moraine piles.

The aquatic resources in this region are highly diverse in both morphology and their respective annual hydrologic cycles. Water here is derived from three main sources: snowpack, groundwater, and rainfall; all of which provide spatial and temporal variation in water source contribution to aquatic features. As snow melts in the spring, meltwater fills the lake, ponds, and streams to maximum capacity. During this time, most habitat patches are connected through a complex network of temporary and permanent streams. As summer progresses, groundwater becomes the primary water source, with many snowmelt derived features completely drying up (Figure 5).

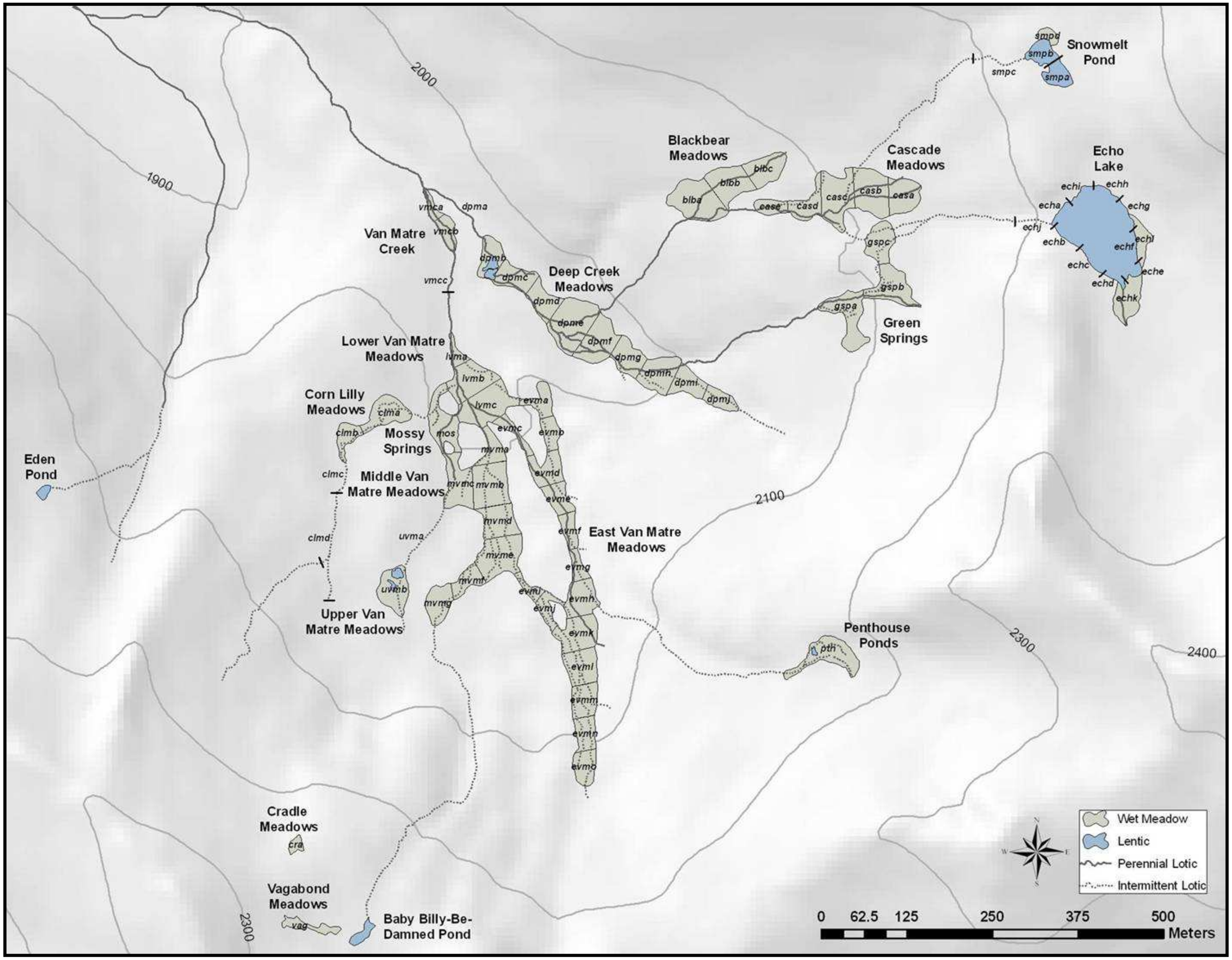


Figure 3. Map displaying the distribution of all aquatic habitat patches within Echo Lake basin, Trinity Alps Wilderness, California. Habitat patches and survey zones are represented by a 4 letter code within each zone: The first three letters represent the patch ID, the last letter represents the zone ID within a specific patch; patches with only one zone have a three letter code identifying the patch name. Stream, pond, and lake zones are separated by black hatch lines. Elevation contours represent 100 meter intervals.

Figure 4. Examples of habitat patches surveyed for Cascades frogs from 2003 to 2007 in Echo Lake basin, Trinity Alps Wilderness, California. Top left: small isolated spring-fed meadow. Top right: large meadow complex with semi-isolated patches connected through a stream network. Middle left: small isolated permanent pond. Middle right: Echo Lake, a medium sized isolated tarn. Bottom left: stream draining a large portion of the basin (note thick peat headwall to the left of the falls). Bottom right: large isolated moderate sloping meadow.

Figure 5. Example of temporal variation in aquatic habitat at SMP (Snowmelt Pond) during the summer of 2003 in Echo lake basin, Trinity Alps Wilderness, California. This temporary pond was used for reproduction by Cascades frogs from 2003 to 2007. frogs conducted extensive migrations to this site annually. Among others, this site dried up completely each year by late October, forcing all ages of Cascades frogs to move to distant over-wintering habitat patches.

We identified 63 individual groundwater spring sources of varying discharge and tenure. Most groundwater sources remained throughout the summers, though some dried in the fall seasons, especially during drier years. Furthermore, we have found as annual vegetation dies in the late summer, some aquatic features correspondingly refill with water via soil percolation. Based on this study, isolated summer rain events had little to no effect on hydroperiod or on recharging drying waterbodies during the summer months. We suspect rain to have a much larger effect on snowpack tenure during rain-on-snow events.

Land Use History

Grazing

The meadows of upper Deep Creek basin were grazed by cattle through a USFS grazing allotment which was terminated after 1978. USFS records indicate that between 1947 and 1978 anywhere from five to132 head of cattle grazed the meadows of Stuarts Fork drainage from June through October each year. Prior to 1947, grazing in the Trinity Alps by both sheep and cattle was largely unregulated and goes back as far as the late 1800s when major gold mining was still occurring in the area. Potential long-term effects of grazing, especially on meadow system hydrology and erosion, have not been studied.

Introduced Fishery

Based on California Department of Fish and Game (DFG) region one stocking records, the earliest written record of non-native trout introduced into Echo Lake occurred in 1930 (B. Aguilar, pers comm.). This record indicates that 10,000 eastern brook trout and 5,000 rainbow trout (*Oncorhynchus mykiss*) were planted during this event, representing densities of 1.3 fish/m^2 of lake surface area. During the summer of 1942, three stocking events occurred at Echo Lake, which totaled an impressive 18,400 brook trout, or 1.6 fish/m^2. In the following decades, stocking numbers were reduced drastically, ranging from 780 to 4,000 fish per year, though the lake was not stocked on an annual basis. The vast majority of fish planted were brook trout; rainbow trout were stocked on only a few occasions. In 1999, Echo Lake was pulled off the stocking rotation by DFG after being assessed multiple times as a poor fishery (B. Aguilar, pers. comm.) though a self sustaining population of brook trout has since persisted. Based on our recent snorkel surveys, and gill net surveys conducted by Karen Pope, rainbow trout appear be extirpated from Echo Lake basin. Unlike brook trout, it appears rainbow trout are unable maintain a self-sustaining population in Deep Creek basin without periodic stocking efforts.

STUDY METHODS

Site Selection

Upper Deep Creek Basin was selected for this study due to a combination of unique characteristics. Prior to this study, in 2002, a persistent population of Cascades frogs was found to exist here, with many breeding sites distributed throughout the area. Upon further examination, the area was also found to have a mosaic of potential aquatic habitats (lake, pond, stream and wet meadow) for Cascades frogs (Figure 4), and thus allow for a detailed assessment of resource use among a full spectrum of potential habitats. Also, non-native brook trout have a limited distribution in the Basin, so species could be studied in areas with and without fish. Last, this region currently has minimal anthropogenic impact. The area is fully protected under wilderness regulation, and is very remote (nearest trailhead ~10 km) with limited human impact due to its steep, inhospitable trail access.

Study Duration

This study spanned five years from the spring of 2003 to the spring of 2007. The majority of frog and snake census work occurred from 2003 through 2006, spanning the entire annual active period of both Cascades frogs and garter snakes (May through October). This study also encompassed the entire Cascades frog breeding season in 2007 (April to July). No garter snake data was collected in 2007. Long-term mark-recapture and reproduction data on Cascades frogs is anticipated to be continued beyond the duration represented in this report.

Capture Surveys

From 2003 through 2006, systematic visual encounter surveys (VES) for Cascades frogs and garter snakes were conducted approximately every two weeks throughout the annual active period. In 2007, surveys were conducted from late April until July. Although surveys for Cascades frogs occurred throughout the entire upper Deep Creek basin, the majority of the study was restricted to the south sub-basin (342.2 ha), hereafter Echo Lake basin. Regular surveys were concentrated at all fifteen designated habitat patches within Echo Lake basin (Figure 3). The north sub-basin, hereafter Siligo basin, was surveyed on a limited basis along with four other isolated patches adjacent to, though outside of, upper Echo Lake basin. These isolated patches include Red Mountain Meadows, Billy-Be-Damned Lake, Deer Lake, and an unnamed meadow system and adjacent pond, hereafter referred to as Atlantis (Figure 2). Of these proximal sites, Red Mountain Meadows was surveyed all years and received the most effort for proximal sites. This isolated meadow system is located in Stony Creek basin and is greater than 800 m from the nearest Cascades frog habitat in Echo Lake basin.

Surveys were conducted during calm and warm conditions, which are most effective for detecting diurnal herpetofauna in temperate regions (Crump and Scott 1994, Thoms et al. 1997). Most surveys were conducted between 1000 and 1900 h, and occurred only when a site was exposed to direct sunlight. Adverse weather conditions were avoided, especially when wind and rain limited visibility, or when air temperatures were extremely low for a given season. VES search procedures were adapted from Crump and Scott (1994) and Thoms et al. (1997) where one to two observers walked the perimeter of all lentic habitats and the banks of all streams. The two lentic sites in the basin with surface areas greater than 0.2 hectares (ECH and SMP), were surveyed utilizing two surveyors in tandem due to the complex irregular shorelines and adjacent talus fields. One surveyor walked the shallow littoral zone, while a second searched on land within two meters of the shoreline. Streams greater than 0.5 m wide were also searched in tandem, with one surveyor walking each bank. Flooded portions of meadows were searched using a zigzag pattern (Thoms et al. 1997) after all confined lentic and stream habitats were searched. As each season progressed, riparian vegetation in meadow streams increased dramatically in height, limiting a surveyor's vision of the channel in some areas. While surveying, dip nets were used to sweep any dense riparian vegetation away from the concealed channel in order to visually search the stream for herpetofauna. We attempted to capture all juvenile and adult Cascades frogs. However, young-of-the-year frogs were not captured to reduce possible handling and marking stress on metamorphosing individuals going into their first winter. All age classes of garter snakes were captured.

Measuring and Marking

All Cascades frogs and garter snakes were captured by hand or with a dip net. When captured, individual frogs were placed in numbered pint size plastic freezer bags filled with water. Garter snakes were retained in cotton sacks. Capture locations were marked with a numbered pin flag which corresponded to the numbered bag so individual animals could be returned to their exact capture location after processing. All frogs were weighed (g) with a 60 g Pesola spring scale (accuracy ± 3%). Snout-urostyle lengths (SUL) were measured to the nearest mm using metric dial calipers (accuracy ± 1 mm). Measurements of SUL were standardized by "maxing out" SUL lengths of individual frogs. This was achieved by placing frogs on a flat surface and applying gentle lateral and vertical pressure on the animal when measuring. This method of measurement minimalized SUL length variation by not allowing frogs to contract during measurement. Sex of individuals (≥ 45 mm SUL) was determined by the presence or absence of nuptial pads that exist on the thumbs of maturing males. Since some frogs received PIT tags prior to the size that sex could be determined (< 45 mm SUL), subsequent captures of many individuals revealed the sex for a large subset of PIT tagged juveniles. Garter snakes were also weighed with Pesola spring scales, and measured (snout-vent) with a fabric tape to the nearest mm.

Immature Cascades frogs (< 40 mm SUL) were marked from 10 June 2003 to 11 October 2005 using a biocompatible Visual Implant Elastomer (Northwest Marine Technologies, Shaw Island, Washington, USA). Visual Implant Elastomer (VIE) has no reported negative effects on survival, growth, and behavior of other amphibian species, and is recently preferred over toe clipping (Nauwelaerts et al. 2000, Bailey 2004, Wahbe et al. 2004). All new captures were cohort marked with a color and digit code so individuals could be identified to a specific habitat patch. Cohort marks for each site were changed each year so frogs could be identified to the patch and year marked. We did not mark any juvenile frogs with VIE after 2005 due to logistic constraints.

Cascades frogs ≥ 40 mm SUL were marked individually with Passive Integrated Transponder (PIT) tags (TX1400L, Biomark Inc., Boise, Idaho, USA) throughout the study period. PIT tags have recently become a method of choice for marking medium to large size anurans; see Ferner (2007) for a review. PIT tags were inserted into a 2 mm wide, V-shaped incision through the dermal tissue using stainless steel dissecting scissors sanitized in 90% ETOH prior to each marking. The incision was located on the dorsal surface, anterior and lateral to the sacral hump.

We marked garter snakes beginning in 2004 and continuing through 2006. Garter snakes ≤ 340 mm were marked by ventral scale-clipping similar to Brown and Parker (1976). Garter snakes > 340 mm SVL were marked using PIT tags. PIT tags were inserted ventrally into the body cavity with a sterilized 20 gauge injector one third the snout-vent length of the animal up from the vent. Based on dissection of preserved specimens of a similar species of *Thamnophis*, Keck (1994) suggested this to be the best point of injection to avoid puncturing the stomach or gonad regions of the animal.

Radio Telemetry

We used radio telemetry from 2003 to 2004 to study movement rates, migration routes, and microhabitat use of adult Cascades frogs. We attached BD-2 transmitters (Holohil Systems, Ltd., Carp, Ontario, Canada) to 30 female and 21 male Cascades frogs from 20 June through 3 October in 2003, and 18 June through 10 October in 2004. In 2003, transmitters were fitted to individuals using a polyester ribbon as a waist belt (Pilliod et al. 2002). In 2004, transmitters were fitted to Cascades frogs using glass seed beads threaded with an elastic string as a waist belt (Muths 2003). Transmitters represented on average 4.3 ± 0.15 g of the total body weight, which is well under the 10% of body weight recommended by Richards, et al. (1994). Individuals were tracked for varying lengths of time, but overall, tracking sessions occurred within the months of June through October, encompassing the entire annual activity period for the study area.

Egg Mass Surveys

We conducted weekly egg mass surveys during each spring throughout Echo Lake basin to identify breeding habitat characteristics, total basin-level reproductive effort, and timing of oviposition for each year (Crouch and Paton 2000). On cloudy days, searchers used polarized glasses to avoid surface glare at sites. Individual egg masses were labeled with numbered pin flags or with a small injection of VIE in the center of the mass to avoid double counting on subsequent visits. In order to describe microhabitats used for oviposition, variables including surface area, depth and water body type (pond, spring pond and lake) were collected as well as attachment substrate, depth of water and submerged depth at individual egg masses.

Garter Snake Diet

From 2003 to 2006, garter snakes were palpated to force regurgitation of food in their digestive tracts as described by Fitch (1987). The number, species, and life stage of stomach contents were recorded. Adult female snakes that showed signs of being gravid were not palpated.

Fish Surveys

Fish presence at Echo Lake was determined by gill netting (K. Pope, unpubl. data, USFS/UC Davis) Fish distribution and density were also determined utilizing bounded snorkel counts within all permanent streams (Hankin and Reeves, 1988) during the summer of 2005. Three counts were conducted in each habitat unit (riffles, runs and pools) by three different divers with 15 minutes of inactivity between each count. Water visibility during dive sessions was exceptional and care was taken to move slowly into habitat units from below to avoid startling fish.

All animal care and handling procedures met requirements of the Humboldt State University IACUC (Protocols: 02/03.W.106A and 03/04.W.66-A).

Basin Mapping

Important spatial attributes, including water body shoreline perimeters, wet meadow perimeters, stream networks, spring source locations and Cascades frog individual capture locations and breeding sites were mapped using a global positioning system (Tremble GeoExplorer III®, Sunnyvale, California). Defined stream channels were mapped by walking a single path throughout the length of each channel. Wet meadow perimeters were pre-determined by placing pin flags at the edge of the wetted area and then walked with the GPS to map perimeters. All permanent streams and large ponds within these meadow perimeters were also mapped. Additionally all individual spring origins were mapped with a point location at the source of discharge. All spatial data was differentially corrected using a nearby base station and further ground-truthed with high resolution satellite imagery and site visits to maximize mapping accuracy.

Habitat Inventory

In this report; we define a basin as a terminal headwater catchment that is separated from another by a ridge. These criteria account for a much finer watershed scale than the CalWaters scale (as defined by the California State Department of Water Resources- CalWaters GIS coverage) used commonly by state and federal agencies . We avoided using the Calwaters defining criteria because the terminal portions of Upper Deep Creek are actually two separate basins (Figure 2) with physical barriers that limit migration and dispersal of Cascades frogs.

We characterized and measured all lentic features and 83% of all lotic features in Echo Lake basin. We did not measure 3.6 km of streams that were mainly isolated steep gully features away from the 15 core habitat features. These measurements were collected three times (spring, summer and fall) within each patch and summarized by pre-established habitat zones. In meadow systems, zones were approximately 50 m long belts of varying widths that extended up the meadow. Stream and lake zones were based on 50 m transects along the stream or lakeshore. Ponds were characterized as spring fed or runoff ponds based on their respective water sources. Spring fed ponds were directly connected to, or formed by, a nearby spring source whereas runoff ponds were depressions filled by spring snowmelt meltwater or rainfall.

Lentic sites (e.g., spring pond, runoff pond and lake) measurements included surface area and maximum depth for each visit. For lotic sites (e.g., springs and streams), measurements included surface area, mean depth and mean width for each visit. The spring season habitat inventory was collected during peak snowmelt runoff and represents the maximum catchment capacity of each patch. Summer and fall inventories were conducted during the middle of each season respectively to represent average conditions during these seasons. Habitat data was collected in 2003. Because four years (2003-2006) had above average snowpack (170%, 125%, 120%, and 251% respectively), these measurements represent conditions for moderate to wet water years.

Weather

Air temperature was continuously recorded throughout each season from 2003 through 2006 by an automated weather station (Onset Inc.) set up 1.5 m above ground in a meadow at mid-basin elevation (2070 m). Air temperatures were recorded once per hour throughout each season. Precipitation was collected by an automated tipping bucket from 2003 to 2005.

Vandalism to the station by a black bear kept us from collecting precipitation data in 2006 and 2007.

Analysis Procedures

We used S-PLUS v. 4.5 (S-Plus 1997) and NCSS v. 2004 (Hintze 2001) to perform all statistical operations. Error calculations reported with mean values represent ± 1 standard error. All statistical tests were considered significant at $\alpha < 0.05$. All spatial applications including kernel analysis were completed in a geographic information system (ArcGIS 9.0, ESRI 2004) using spatial analyst and Hawth's Tools, an ArcGIS spatial analysis extension (Beyer 2004).

Cascades Frogs

In order to address ecological questions based on season (spring [breeding], summer and fall), seasonal date cutoffs for Cascades frog captures were established. Due to wide geographic variation in Cascades frog reproduction timing in Echo Lake basin (up to 6 weeks), we established cutoff dates between breeding and summer seasons independently at each patch. Controlling for patch specific reproduction timing allowed us to more accurately describe shifts in behavior and habitat use across an elevational gradient. Since Cascades frogs are explosive breeders (< 10 days) at individual patches, the beginning of summer at each patch was defined as one week after the last egg mass was laid. Any captures at individual patches prior to this time were considered within the breeding season. Alternatively, a cutoff date defining separate summer and fall/winter seasons was not defined at individual patches. We established the fall/winter season as September 15th annually. By this date, most seasonal summer habitats were dry, air temperatures were cool, and most frogs were staging at over-wintering locations.

Individual frogs were placed into one of three age classes, and were sexed when possible, so age and gender could be addressed in the analysis. Age categories included: young of previous year (YOPY), juveniles, and adults. We defined YOPY as frogs that have survived their first winter and are living in their second year of life. Since young Cascades frogs grow relatively fast, size cutoffs separating YOPY from juveniles were generated using data on length frequency histograms of captures for each season separately. Like many other anuran species, Cascades frogs exhibit sexual size dimorphism as adults (Monnet and Cherry 2002), with females attaining larger sizes than males. Although male Cascades frogs developed nuptial pads at 45mm SUL in this study area, we considered this as a secondary sexual characteristic and used reproductive behavior to determine age class instead. During each breeding season (2003-2006) only active adult frogs exhibiting courtship behavior congregated around breeding sites. Based on minimum sizes of these animals, we determined the smallest size of adult frogs to be 50 mm SUL for males and 58 mm for females. Furthermore, all measured amplexing individuals ($n = 66$) as well as fall females showing gravidity, exceeded our minimum size cutoffs.

Based on captures, female Cascades frogs were captured much less than males in the spring, but became more active relative to males during mid to late summer. To investigate the relationship between date and the probability of capturing an adult female frog we used a single variable logistic general additive model (GAM). A GAM was used because the relationship between the independent variable and the response variable was nonlinear. GAMs relax the assumption that the relationships between the dependent variable and independent variable are linier by estimating a nonparametric smooth function (loess) to describe relationships (Cleveland and Devlin 1988, Hastie and Tibshirani 1991). In addition, we used a similar GAM to determine if all ages of Cascades frogs were found using streams in different proportions relative to lentic habitats throughout the active period (May to October) by basing habitats at individual captures as a binary variable (lotic or lentic).

We summarized the total surface area of water in each of the 15 patches in Echo Lake Basin to determine how much water was available for breeding, summer and winter seasons. We also determined the proportion of water available for the summer and winter season relative to the maximum in the spring. Maximum depths by patch were determined for the winter season and represent the deepest water feature available in a patch for over-wintering.

We ranked each habitat zone within patches as breeding, summer foraging, or over-wintering habitats. These categories were based on seasonal hydrology, the presence of egg masses, and the presence of frogs during a given season. Many zones were used for multiple seasons so rankings were based on the total use of each zone over all seasons.

Linier regression was used to explore the relationship between annual snowpack and initiation of breeding for Cascades frogs at both low elevation (DPM), and high elevation (ECH) sites. We used the May 01 average instead of the traditional April 01 average because late spring snow accumulation could greatly influence reproductive timing for Cascades frogs.

We summarized microhabitat variables for radio telemetered frogs. These included substrate and cover objects, as well as maximum water depth within one meter of the frog, and minimum distance to water. To avoid pseudo-replication, proportions of substrate and cover, and mean values water depth and distance to water were calculated for each individual. These values were then averaged across all individuals.

Movement rates of adult Cascades frogs were best described by comparing daily locations of telemetered individuals. Since most radio tracking intervals were once daily, calculated migration rates are likely an underestimate of the frogs true travel but reflect daily activity. We tested average daily movement rates between seasons (spring, summer and fall) and sex using analysis of variance (ANOVA). Post hoc comparisons of groups were performed using the Tukey Kramer multiple comparisons (Zar 1999).

We defined migration as a seasonal or annual movement pattern by adult frogs between two or more habitat patches separated by distances ≥ 100 m. To test if mean migration distances by adult frogs differed by season (breeding, summer and fall), we used the Kruskal-Wallis analysis of variance (ANOVA) on ranks test. Differences between groups were determined by the Bonferroni corrected Kruskal-Wallis Z test. We then used Mann-Whitney U tests, to determine if mean movement by season differed between male and female frogs. The leptokurtotic nature of our movement data warranted the use of these non-parametric tests (Zar 1999).

In this paper we define dispersal as a permanent directed movement by juvenile frogs to a separate habitat patch greater than 100 m away. We determined net dispersal of juvenile frogs by using their first capture location, and calculated the distance to their furthest respective capture away from the initial location. Net dispersal is a conservative displacement estimate because it eliminates variation based on multiple capture events that inflate actual distances traveled between initial and furthest locations. Mean dispersal was calculated using only animals that moved distances ≥ 100 m. We tested the difference in elevation for inter-basin dispersing frogs using a paired t-test.

Site fidelity was indicated using animals that were found in the same patch in different years. Proportions for Cascades frogs showing annual site fidelity were determined from one to three years for both age and gender from 2003 to 2006. One year of site fidelity equaled one year between captures (e.g., 2003-2004). Two years of site fidelity equaled two years between captures (e.g., 2003-2005). Three years of site fidelity equaled three years between captures (e.g., 2003-2006). To avoid pseudo-replication, individual animals were only counted once per time category. For example: if the same frog was captured four straight years, it was only included in each 1, 2, and 3 year categories once. We used Chi-square tests to determine if the proportion of adult and juvenile animals exhibiting site fidelity changed from one to three years. 2007 data was omitted from this analysis.

Garter Snakes

We compared the overall net displacement of both garter snake species by calculating the minimum straight-line distance between initial and furthest locations of snakes captured two or more times. Our garter snake movement data was highly leptokurtotic, so we used the nonparametric Mann-Whitney *U* test (Zar 1999) to test for differences in movement between species. Diet samples were keyed down to species and categorized into respective life stages.

Brook Trout

We calculated brook trout abundance in Deep Creek Meadow (DPM) using the bounded counts formula (Dolloff et al. 1996). The estimated number of fish present, $\hat{N}$ is calculated according to the formula:

$$\hat{N} = \sum \left(2N_m - N_{m-1}\right)$$

where N_m is the largest and N_{m-1} the second largest count in a series of passes through the sample unit. All sample unit abundance estimates were then summed for total fish abundance. We then calculated the density of fish per meter of stream by dividing the total estimated abundance by the total length of stream surveyed.

Species Density and Distributions

Part of this study's focus was to address how non-native fish may potentially impact a Cascades frog population at the whole-basin scale. We summarized fish distributions relative to Cascades frogs by calculating the number of uniquely marked frogs that moved between sites with and without brook trout.

Since Cascades frogs used streams often during summer foraging, we compared their summer capture densities between two stream reaches (each 190 m in length); one with a dense population of brook trout and one without any fish. Both streams were located within 100 m, had similar slopes, discharges and riparian vegetation characteristics. Each stream was also located within 50 m of established Cascades frog breeding habitats.

To compare species overlap for brook trout, garter snakes, and Cascades frogs we calculated 100% fixed kernel utilization distribution (UD) estimates (bandwidth: 100) for each species. A kernel UD estimator produces a nonparametric distribution representing the likelihood of finding an animal and the intensity of use by that animal at any particular location (Worton, 1989; Marzluff et al., 2004). Although kernel estimates are most commonly used to approximate an individual animal's home range (Worton, 1989; Millspaugh et al., 2006), we applied them here to all located individuals of a species to visually relate the species' UD to prey distribution. We included only the initial observation of an individual per year to remove spatial dependence related to multiple locations of the same individual (aquatic garter snakes: $N = 69$, common garter snakes: $N = 87$). To quantify the spatial association of garter snakes and prey, we mapped Cascades frogs and brook trout locations in the basin. For Cascades frogs we used the same UD analysis as used for the snakes. Utilization distributions were not calculated for trout because trout distributions could be more accurately displayed using a bar graph, given that they were found only in a short stream segment with distinct physical barriers. We used 2 X 2 contingency tables to compare the overlap of the 95% distribution kernels of the garter snake species with the distributions of the prey. For this analysis we used 95% kernels instead of 100% to better restrict the distribution fit closer to the actual core use areas (Millspaugh et al., 2006). The Bonferroni correction was applied for multiple comparisons.

RESULTS: CASCADES FROG CAPTURES AND ECOLOGY

Surveys and Frog Captures

A total of 568 systematic visual encounter surveys over 44 census periods were conducted in Echo Lake basin (Appendix A). These surveys encompassed the entire annual active period of Cascades frogs (May through October) from 2003 through 2006 and during the spring of 2007. Overall, the study resulted in 6685 captures over the five year period (Appendix B). Of the 6,685 captures, a total of 1,758 individuals were identified and marked (Appendix A): 1,098 with PIT tags, and 1,016 with VIE. Furthermore, 356 individuals tagged with VIE received PIT tags after attaining larger sizes. Overall, the number of annual Cascades frog captures was consistently higher during the mid-summer than spring or fall; most captures occurred from mid-July to mid-August when daily average temperatures were highest and the frogs were most active (Figure 6).

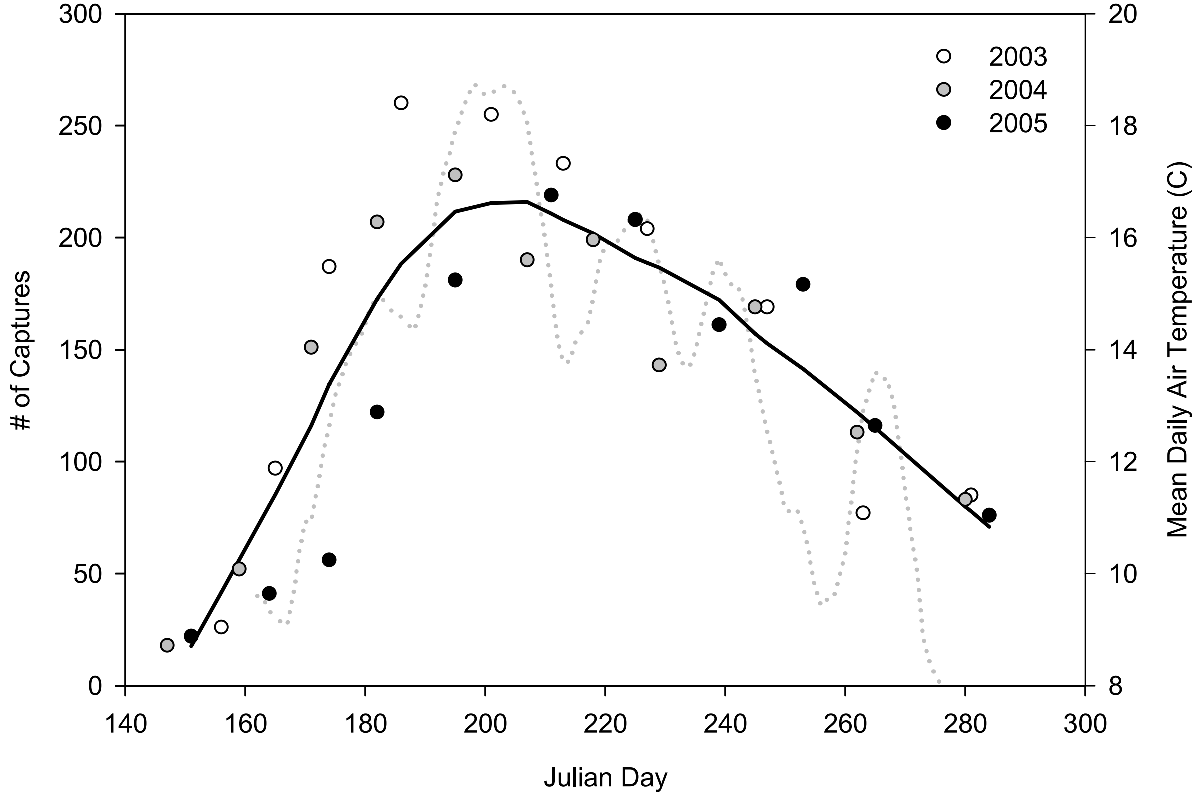


Figure 6. Total number of Cascades frogs captured in 32 census periods for years 2003 to 2005 in Echo Lake basin, Trinity Alps Wilderness, California. All 2006 and 2007 counts were omitted due to unequal survey effort. Census date was calculated as the median survey date of a given census period. Only complete regular surveys are represented; incidental and partial survey captures were omitted. Solid black line represents the estimated regression line for captures using a loess nonparametric smoothing function. Dotted line represents the mean air temperature from 2003 to 2005 summarized daily from seven day running averages.

The sex ratio of 647 PIT-tagged adult frogs was bias toward males (1.6 males: 1 female; 399: 248 respectively). This bias was largely attributed to size difference at sexual maturity, with males maturing younger and at a much smaller size (50 mm) than females (58 mm) (Figure 7). The mean length of adult frogs was 56 mm for males and 68 mm for females. The mean weight of adult frogs was 18.5 g for males and 30 g for females. Among adults, the probability of capturing a male vs. female frog changed significantly throughout the annual active period (Figure 8). During the spring, the majority of captures were adult males found to be concentrated around breeding sites. Adult females remained cryptic throughout the breeding season, with most captures found either in amplexus or as spent animals leaving breeding sites. In contrast, female frogs were captured during the fall at significantly greater proportions, with adult males becoming largely inactive at over-wintering locations. These results suggest that, due to their size (many gravid female frogs weighed over twice that of males), gravid females remained active late into the fall (late September/ October) due to higher energy demands for egg production and over-winter survival.

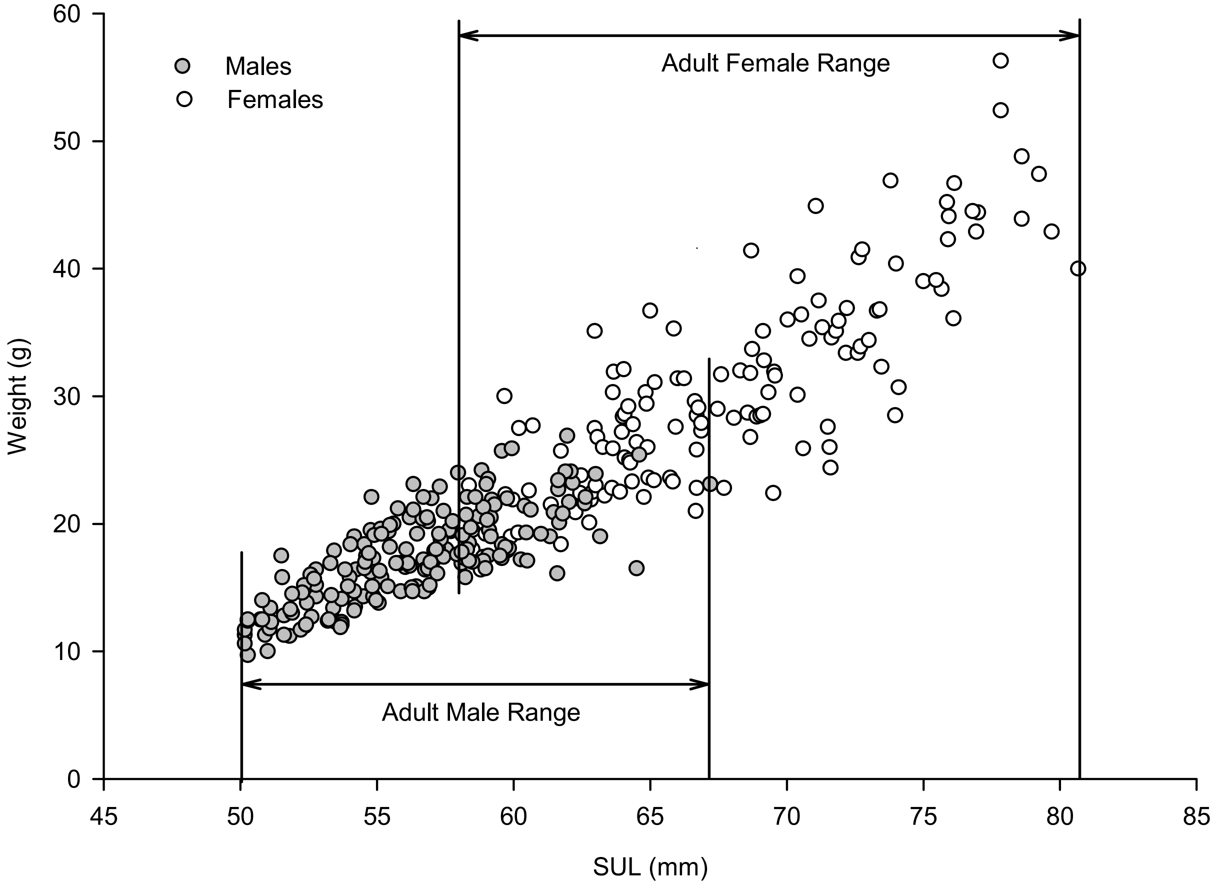


Figure 7. Length to weight relationship of individual adult male (*n* = 187) and adult female (*n* = 137) Cascades frogs in Echo Lake basin, Trinity Alps Wilderness, California, from 2003 to 2006. Minimum length cutoffs for each sex were established based on reproductive condition and activity. Adult male sizes ranged from 50 to 67mm where adult females ranged from 58 to 81mm.

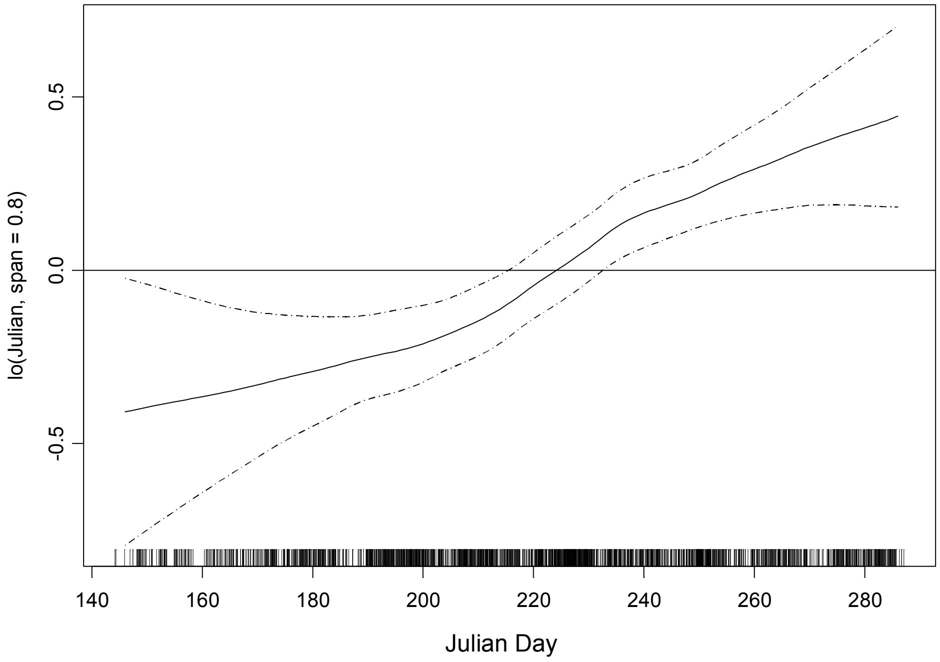


Figure 8. Estimated effect of Julian day on the probability (including approximate 95% confidence intervals) of capturing an adult female relative to an adult male Cascades frog from 2003 to 2006 in Echo Lake basin, Trinity Alps Wilderness, California. Zero line indicates mean effect level where 95% bounds above or below the line indicates significance. Bounds below the effect line indicate a significantly lower probability of capturing adult females. Bounds above the effect line indicate a significantly higher probability of capturing adult females. Hatch lines at the bottom of graph represent individual data points.

Resource Dynamics and Habitat Use

Basin Scale

The availability of aquatic resources in Echo Lake basin changed considerably throughout the active period of Cascades frogs (Table 1). During spring, the total surface area of water was 2.58 square hectares, with a total of 588 ponds and 10.4 km of streams measured. Echo Lake contained 1.14 ha of water representing 44% of the available aquatic habitat. After the snowpack disappeared in mid-summer, the amount of available aquatic resources reduced to 1.80 square hectares, with 253 ponds and 5.8 km of stream measured. Echo Lake contained 64% of the aquatic habitat available in the basin in mid-summer. As frogs staged at wintering areas in the fall, aquatic habitat features reduced further to 1.57 square hectares of surface water, with 146 ponds and 2.9 km of stream measured. Echo Lake contained 78% of the aquatic habitat available in the basin during the fall seasons.

Table 1. Summary of the total surface area of water by patch and season for Echo Lake basin, Trinity Alps Wilderness, California from June to October of 2003.

	Season:	Breeding	Summer		Winter		
Patch Id.	Patch Type	Maximum Water SA (m^2)[a]	Water SA (m^2)[b]	% of Maximum SA[c]	Water SA (m^2)[b]	% of Maximum SA[c]	Max Winter Feature Depth (m)[d]
BLB	Meadow	487	221	45	149	31	0.25
CAS	Meadow	822	397	48	204	25	0.88
CLM	Meadow	430	157	37	0	0	–
DPM	Meadow	3553	2240	63	1145	32	1.24
EVM	Meadow	1391	446	32	361	26	0.62
GSP	Meadow	794	568	72	178	22	0.36
LVM	Meadow	646	265	41	256	40	0.62
MOS	Meadow	433	271	63	89	21	1.15
MVM	Meadow	1294	333	26	191	15	0.5
UVM	Meadow	581	381	65	168	29	0.34
PTH	Meadow	388	217	56	186	48	0.7
ECH	Lake	11,698	11,527	99	11,465	98	5.1
EDN	Pond	278	215	77	140	50	0.8
SMP	Pond	2483	489	20	0	0	–
VMC	Stream	477	255	53	201	42	0.31
Mean:		1717	1199	53	982	32	1.0
Total SA By Season:		25,755	17,982	70	14,735	57	
Total SA By Season without ECH:		14,057	6455	46	3270	23	

[a] *Total surface area of water features by patch during the breeding season when water-bodies have maximum catchments and streams are flowing at bankfull capacity.*

[b] *Total surface area of water features by patch during the mid-summer and late fall seasons.*

[c] *Percent of the spring maximum surface area of water features by patch in the mid-summer and late fall seasons.*

[d] *Maximum depth of the deepest water feature by patch during the late fall season.*

Based on these measurements, the total surface area of water in the basin was reduced by 43% between the spring and fall. However, when Echo Lake is subtracted, the amount of available aquatic habitat in the basin reduced by 77% over this period. Furthermore, individual habitat patches experienced variable losses of water, with 50 to 100% of all patch areas drying (Table 1). Two patches (CLM, SMP) dried completely. Finally, six of 15 formally connected patches became isolated due to the complete drying of connecting streams.

Zone Scale

Overall, 56% of all habitat zones were classified as perennial, and contained aquatic features year round. The remaining habitat zones (44%) were ephemeral, with all features drying completely by the fall. Out of 73 zones, 23 (32%) were used for breeding, 73 (100%) were used during the summer and 41 (56%) were used for wintering (Figure 9). Since many zones dried completely by the fall, over-wintering habitats were sometimes limited to features in isolated zones within patches (Figure 9).

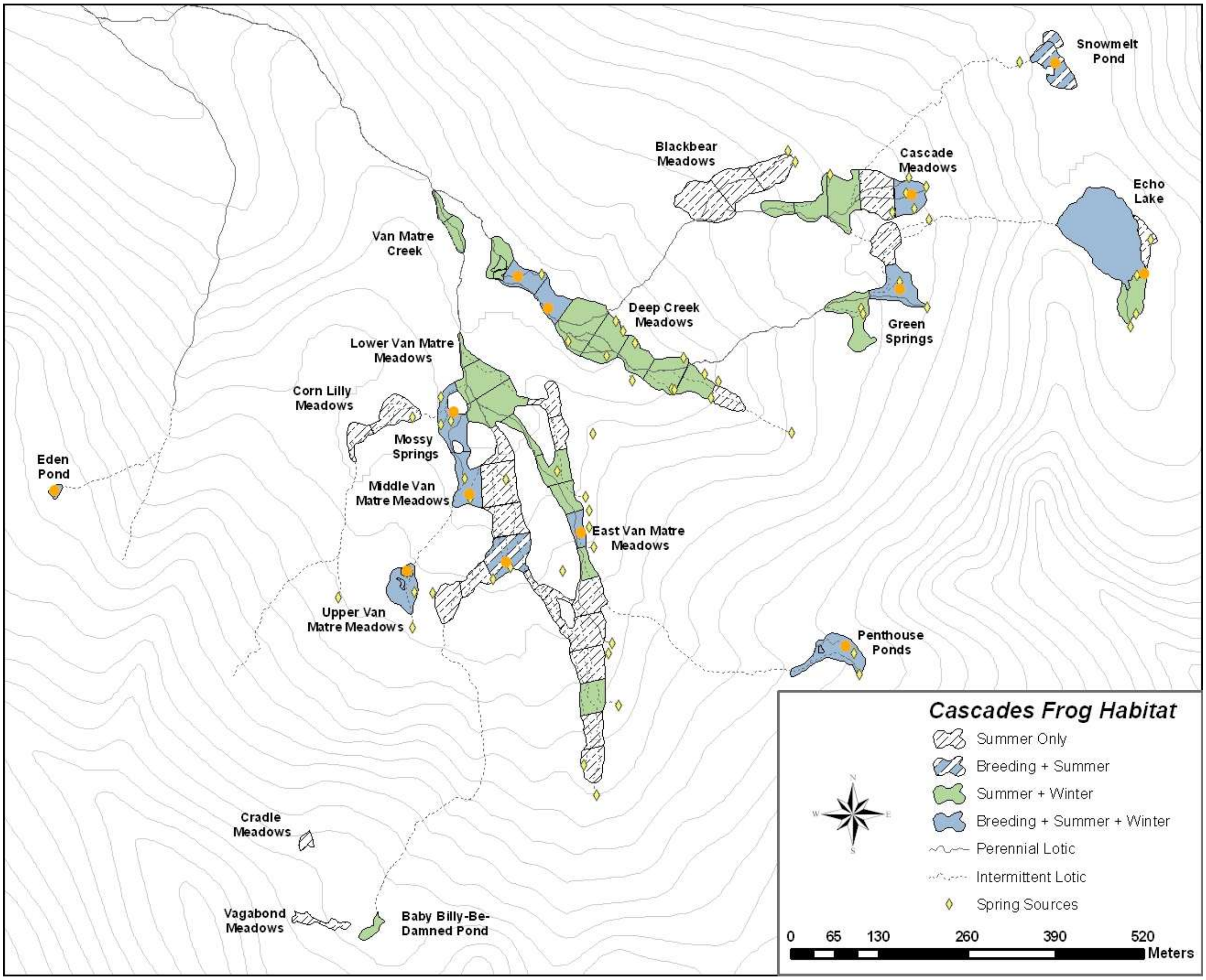


Figure 9. Map of Echo Lake basin, Trinity Alps Wilderness, California, displaying seasonal hydrological properties of habitat zones used by Cascades frogs from 2003 to 2007. Cross hatched zones and dotted stream segments dried completely by late summer so they were unavailable for wintering use. Areas within green colored zones and solid line streams were used for both summer and wintering habitats. Areas within solid blue zones were used year round. Yellow diamonds indicate where groundwater springs emerge. Orange circles represent traditional breeding areas used by Cascades frogs.

Breeding Habitats

From 2003 to 2007, 38 individual lentic sites were used for reproduction by Cascades frogs throughout Echo Lake basin, including 28 spring-fed ponds, nine runoff ponds, and one lake. These breeding sites were located in 12 distinct areas (close aggregations of breeding features within 50 m) throughout the basin containing from one to nine individual sites (Figure 9). In meadows, many breeding ponds were in close proximity or even hydrologically connected during the spring; whereas, ECH, SMP, and EDN were relatively isolated and lacked adjacent breeding habitats. The minimum distance separating breeding areas ranged from 114 to 528 m (mean = 245 m).

The mean maximum depth of the 35 meadow breeding ponds was 0.48 ± 0.03 m, (range 0.15-0.87 m). The three large isolated sites had greater maximum depths: EDN (1.3 m), SMP (1.47 m), and ECH (5.1 m). Surface area of meadow breeding ponds varied widely, ranging from 2.5 to 183 m^2, mean = 22 ± 5.8 m^2. We collected substrate data for 239 egg masses. Most of these egg masses were attached to dead grass or sedge (80%). We observed fewer egg masses attached to other substrates: dead wood (6%) and rock (4%). Twenty-three (10%) egg masses were not attached to any substrate. A total of 92 (33%) egg masses were oviposited communally in clusters containing as many as nine individual masses. Most egg masses were oviposited in shallow alcoves or on shallow bench features within the breeding site. Mean water depth at oviposition locations (N = 121) was 10.3 ± 0.5 cm. The mean depth each egg mass was found below the surface at these locations was 1.6 ± 0.3 cm. Although thirty-eight individual sites were used for breeding, 197 (72%) egg masses were found in 11 sites used for breeding all five years (Table 2). Conversely, only 4% (13) of the total egg masses were oviposited in 12 sites used only one year.

Summer Habitats

Cascades frogs were most widely distributed during the summer. During this time they utilized all available habitats in Echo Lake basin. In addition to perennial habitats, some frogs utilized areas during the summer that completely dried by fall, requiring frogs to move to and away from these habitats annually. Captures, by age class and sex, at both perennial and ephemeral habitats are summarized in Table 3. Annual summer captures of YOPY frogs were strongly associated with habitat zones containing perennial features (up to 85% of total annual captures). This was especially evident for habitat zones with breeding sites, which accounted for 59% of annual YOPY captures. In contrast, only 24% of juvenile frogs were captured in perennial breeding zones during the summer. Juvenile frogs were mostly found in non-breeding perennial zones (46%) and ephemeral summer-only zones (26%) during the summer. Summer captures of both adult male and female frogs were similar, with most captured in perennial habitat zones (76% and 84% of the total summer captures, respectively). The majority of adult male and female captures occurred at non-breeding perennial habitats, indicating directed movement away from breeding sites.

Fall /Winter Habitats

From mid-September through October, as temperatures cooled and ephemeral summer habitats disappeared, most Cascades frogs were found concentrated in areas with adequate water as they staged for over-wintering. At some areas, this would consist of a single isolated spring pond that measured less than one square meter of surface area and were greater than 50 m from the nearest water. Other wintering areas contained multiple habitats in close proximity, or were hydrologically connected. Based on late fall surveys (2003-2006), 69% of all frogs were observed using lentic and 31% using lotic habitats (N = 548). The highest percentage of captures were found in spring ponds (38% ± 8.4) followed by Echo Lake (26% ± 9.0) and runoff ponds (5% ± 3.2). In lotic habitats, overall captures were slightly higher in surface streams (16% ± 4.4) than spring fed streams (15% ± 2.7).

Table 2. Summary of the total reproductive output by Cascades frogs within Echo Lake basin, Trinity Alps Wilderness, California, from 2003 to 2007. Percent totals are the number of egg masses found in each breeding habitat divided by the total number of egg masses produced at all sites and years. Hydrology of breeding features: Pond- sealed bottom, no immediate groundwater spring influence, Spring Pond- immediate groundwater spring influence at source, Lake- surface area > 0.5 hectares. SA is surface area.

Pond Id.	Years Used	Hydrology	Max SA (m)	Max Depth (m)	Elev. (m)	2003	2004	2005	2006	2007	Total	% of Total
CAS3	1	Spring Pond	3.00	0.25	2118	1	0	0	0	0	1	0.36
CAS4	1	Spring Pond	3.10	0.58	2118	1	0	0	0	0	1	0.36
CLM1	1	Spring Pond	3.96	0.15	2008	1	0	0	0	0	1	0.36
DPM5	1	Spring Pond	12.33	0.70	1976	1	0	0	0	0	1	0.36
DPM8	1	Pond	9.46	0.70	1978	0	0	1	0	0	1	0.36
PTH4	1	Spring Pond	6.60	0.38	2182	1	0	0	0	0	1	0.36
UVM3	1	Spring Pond	10.00	0.26	2046	0	0	1	0	0	1	0.36
UVM4	1	Pond	17.40	0.43	2045	0	1	0	0	0	1	0.36
DPM9	1	Pond	7.59	0.27	1976	0	0	0	1	0	1	0.36
CAS6	1	Spring Pond	8.76	0.60	2118	0	0	0	0	1	1	0.36
DPM10	1	Spring Pond	9.68	0.71	1978	0	0	0	0	1	1	0.36
PTH5	1	Spring Pond	12.09	0.44	2182	0	0	0	0	2	2	0.73
Total (1 Year):						5	1	2	1	4	13	**4.73**
DPM7	2	Spring Pond	5.67	0.65	1976	0	1	0	1	0	2	0.73
EVM1	2	Spring Pond	3.24	0.46	2037	1	0	0	0	1	2	0.73
MVM4	2	Spring Pond	12.26	0.28	2036	0	0	0	1	1	2	0.73
CAS5	2	Spring Pond	5.72	0.40	2118	1	0	0	0	1	2	0.73
MOS1	2	Spring Pond	20.00	0.25	1998	1	0	0	0	1	2	0.73
Total (2 Year):						3	1	0	2	4	10	**3.64**
MVM1	3	Spring Pond	38.90	0.55	2014	2	0	1	0	1	4	1.45
GSP1	3	Pond	44.40	0.61	2108	1	1	0	0	1	3	1.09
PTH3	3	Spring Pond	6.61	0.48	2182	1	1	0	0	2	4	1.45
DPM4	3	Spring Pond	69.85	0.52	1976	1	1	0	0	2	4	1.45
DPM3	3	Spring Pond	77.84	0.83	1976	2	0	0	5	3	10	3.64
MVM3	3	Spring Pond	6.70	0.28	2031	1	1	1	0	0	3	1.09
Total (3 Year):						8	4	2	5	9	28	**10.18**
MOS2	4	Spring Pond	10.58	0.28	2000	0	1	2	1	2	6	2.18
PTH2	4	Spring Pond	8.85	0.80	2182	1	1	0	1	1	4	1.45
CAS1	4	Spring Pond	26.19	0.38	2118	2	0	1	1	4	8	2.91
DPM2	4	Spring Pond	5.70	0.35	1976	2	1	3	3	0	9	3.27
Total (4 Year):						5	3	6	6	7	27	**9.82**
DPM1	5	Spring Pond	7.54	0.58	1976	2	3	2	2	7	16	5.82
PTH1	5	Spring Pond	2.47	0.32	2182	1	1	1	2	2	7	2.55
DPM6	5	Spring Pond	8.76	0.87	1976	1	1	3	5	3	13	4.73
GSP2	5	Pond	23.39	0.40	2108	1	2	2	3	2	10	3.64
SMP1	5	Pond	2314.84	1.47	2226	14	14	7	4	19	58	21.09
CAS2	5	Spring Pond	6.77	0.52	2118	1	1	1	1	2	6	2.18
EDN1	5	Pond	278.00	1.30	2132	2	2	4	4	7	19	6.91
MVM2	5	Pond	11.11	0.62	2013	1	2	2	1	1	7	2.55
UVM1	5	Pond	183.07	0.51	2044	2	5	8	4	4	23	8.36
UVM2	5	Spring Pond	71.18	0.45	2046	2	3	4	4	3	16	5.82
ECH1	5	Lake	11381.29	5.10	2215	5	6	3	2	6	22	8.00
Total (5 Year):						32	40	37	32	56	197	**71.64**
Total Egg Mass Production:						53	49	47	46	80	275	**100.00**

Table 3. Mean percent of annual summer Cascades frog captures in Echo Lake basin, Trinity Alps Wilderness, California, 2003 to 2006. Data were summarized by habitat zone hydrologic categories.

	Zone Classifications			
	Perennial (*N* = 41 zones)		Ephemeral (*N* = 32 zones)	
Age Class/ Sex	Breeding Summer Winter* (*n* = 19 zones)	Summer and Winter (*n* = 22 zones)	Breeding and Summer (*n* = 4 zones)	Summer Only (*n* = 28 zones)
YOPY				
Mean Annual % ± SE	59.2 ± 8.2	25.7 ± 9.1	5.11 ± 2.9	9.9 ± 3.5
Range	49.8-75.6	8.5-39.2	0.6-10.5	5.4-16.7
Juvenile				
Mean Annual % ± SE	24.3 ± 1.4	45.9 ± 3.3	3.9 ± 0.8	25.9 ± 2.2
Range	20.8-27.0	38.7-53.1	2.9-6.3	21.3-30.7
Adult Male				
Mean Annual % ± SE	35.2 ± 1.0	41.0 ± 1.5	15.3 ± 2.3	8.5 ± 2.2
Range	33.0-37.4	38.2-44.2	9.7-20.0	4.9-14.4
Adult Female				
Mean Annual % ± SE	38.8 ± 6.1	45.2 ± 10.1	5.8 ± 1.6	10.2 ± 3.0
Range	30.3-57.0	30.3-52.1	4.5-8.2	4.1-18.2

**Includes all Echo Lake zones and captures.*

The deepest available wintering habitat in the basin, besides Echo Lake, was 1.24 m or less. Only three of the 13 patches containing wintering habitats had maximum depths exceeding one meter deep (Table 1). Since many breeding areas offered perennial habitats (Figure 9), many frogs also used these areas for over-wintering. For example, at DPM (zone C) we captured 34 adult frogs during late fall from 2003 to 2006. In subsequent spring seasons, from 2004 to 2007, we recaptured 18 (50%) of these animals engaged in breeding courtship at these sites. At another site (MOS), which becomes hydrologically isolated by ~ 50 m, only two spring ponds remain by the fall. We searched one of these spring ponds on 8 October 2006 and found two juvenile frogs 0.5 and 0.6 m down a 15 cm diameter hole. This spring pond was densely surrounded by a thick moss mat and the two frogs were found partially burrowed into these mosses.

Macrohabitat Characteristics

Immature Age Classes

Overall, macrohabitat use by Cascades frogs in Echo Lake basin varied widely for both age and sex (Figure 10). The majority of egg masses produced annually in the basin were deposited in small shallow ponds (55-78%) followed by large deep ponds (17-33%). In contrast, very few egg masses were deposited annually in Echo Lake (4-12%) and none were observed in streams. Similar to the distribution of egg masses, the majority (58-78%) of annual YOPY captures were found in small shallow ponds suggesting strong site fidelity to natal ponds during the first year after metamorphosis. However, we captured 20-33% YOPYs in streams indicating some movement away from natal sites does occur after the first winter. Like YOPYs, many juveniles (40-44%) were also found at small shallow ponds, though slightly more captures were found in streams (43-52%) than in any other habitat.

Adults

Adult frogs had the highest diversity of macrohabitat use out of all age classes (Figure 10). In contrast to immature frogs, adults were found regularly at Echo Lake and in large deep ponds as well as small ponds and streams. Among adults, females used streams twice as much as males (Figure 10). Based on annual captures, adult male Cascades frogs were found in lentic habitats more often (70-87%) than any other post-metamorphic group. Adult females were captured at stream habitats on average 40% (23-57%) of the time compared to 21% (13-30%) of males.

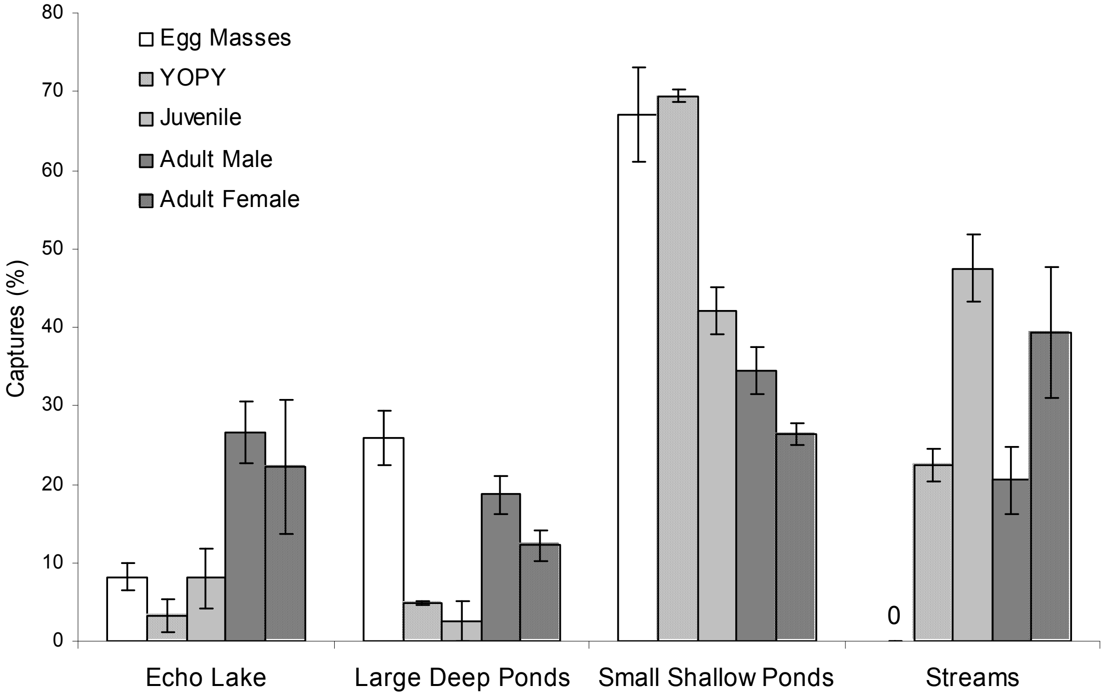


Figure 10. Mean percent of annual egg production and captures of Cascades frogs (separated by sex and age class) found in each macrohabitat category within Echo Lake basin, Trinity Alps Wilderness, California, from 2003 to 2006. The "Large Deep Pond" category represents Snowmelt and Eden ponds. Use proportions are based on 275 egg masses and 4,838 frog captures. The YOPY (young-of-previous-year) age class is represented from 2003 to 2005, although present, none were captured in 2006.

Seasonal Shifts in Macrohabitat Use

Although Cascades frogs appeared to use habitats in different proportions based on age and sex (Figure 10), overall use varied from lentic to lotic habitats throughout the annual active period for all post-metamorphic age classes. For example, frogs were captured at significantly higher proportions in stream habitats during the summer than in the spring (Figure 11). During the spring, the majority of captures were associated with lentic sites used for breeding and over-wintering. As summer progressed, many frogs moved to stream habitats. Fall captures showed no significant preference for either lentic or lotic habitats. Since Cascades frogs are considered strict lentic breeders in this region, this shift in habitat use from lentic to lotic sites during the summer further suggests that post-metamorphic frogs use a variety of habitats during the summer when habitat availability is at is peak.

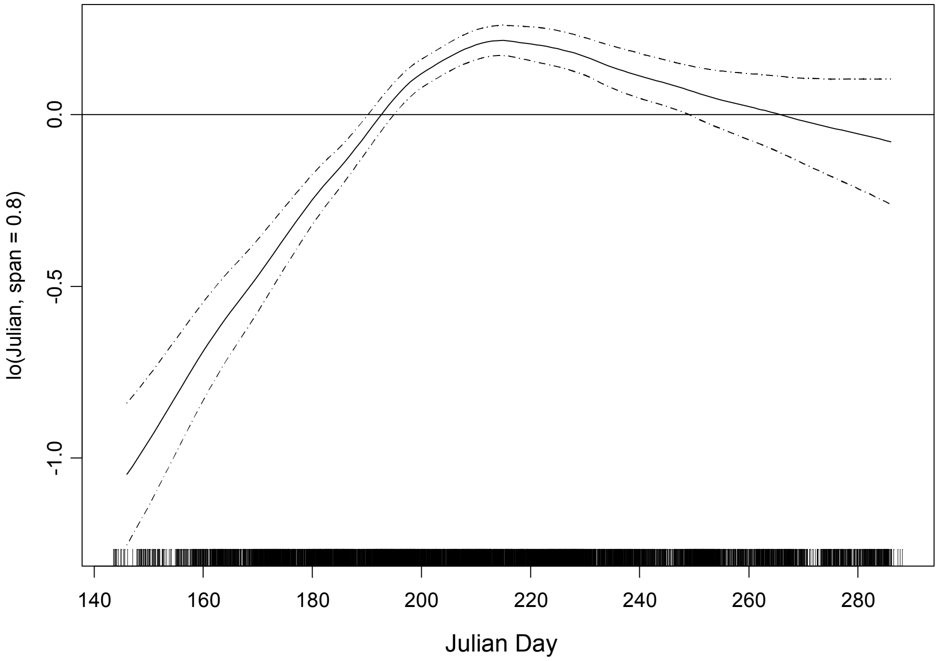


Figure 11. Estimated effect of Julian day on the probability (including approximate 95% confidence intervals) of finding post-metamorphic Cascades frogs in lotic habitats from 2003 through 2006 in Echo Lake basin, Trinity Alps Wilderness, California. Zero line indicates mean effect level where 95% bounds above or below the line indicates significance. Hatch lines at the bottom of graph represent individual data points.

Microhabitat Characteristics

Non-migrating adult Cascades frogs were found to be highly aquatic and strongly associated with riparian areas. Utilizing daily telemetry locations, we found individuals in water 55% of the time (*N* = 51, 970 locations). In 2004, water depths recorded within a meter of each frog location averaged 0.29 ± 0.03 m and ranged from 0.13 to 0.78 m deep (*N* = 30, 482 locations). Also during this year, the average mean distance terrestrial frogs were found from water was 0.54 ± 0.23 m (*N* = 30, 509 locations). Only 14 locations for eight individuals were found upland greater than three m from water (*N* = 970 locations), all of which were during overland migration events. The farthest location from water that a radioed frog was observed was 75 m which occurred during an August rain event (see movement section below). Substrate and cover use by telemetered frogs is summarized in Figure 12. Substrates used by telemetered frogs was dominated by grass and sedge (40%) followed by silt (21%) and boulders (14%). Most frogs were difficult to find and hidden under various cover objects. For example, upon visually locating frogs during each tracking session, we observed them an average of 42 ± 0.03% of the time without looking under, in, or disturbing cover objects to receive a visual on the individual. The majority of frogs that were hidden from view used grasses and sedges (58%) followed by boulders (14%) and undercut banks (8%) as cover objects. Five radioed frogs were found using underground rodent burrows 0.7 to 20 m from water for a period of one to three days. Destruction of one burrow (due to suspected snake predation) revealed a healthy inactive frog at 0.55 m from the burrow's opening.

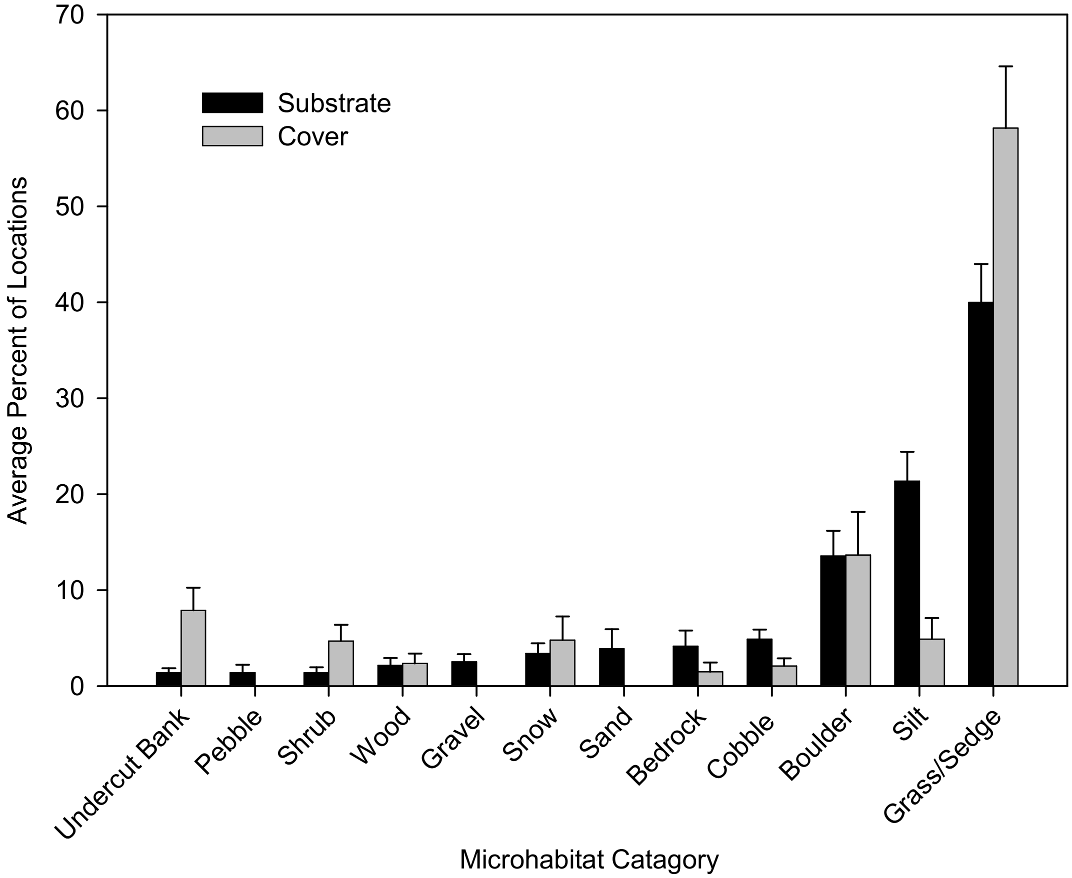


Figure 12. Substrate (*N* = 933) and cover microhabitats (*N* = 394) used by 51 radio telemetered Cascades frogs from 2003 to 2004 in Echo Lake basin, Trinity Alps Wilderness, California. Bars represent the average mean proportions by habitat type for all radioed Cascades frogs.

Cascades Frog Spatial Ecology

Adult Movements and Patch Fidelity

Although some adult frogs exhibited strong seasonal and annual site fidelity to specific patches, others had distinct migration patterns among separate breeding, summer foraging and wintering habitats. Over the duration of this study a substantial proportion of the adult Cascades frog population in Echo Lake basin completed extensive movements among and between different habitat patches (Figure 13). This section summarizes movement rates, routes, and annual migration patterns between seasonal habitat patches of adult frogs from 2003 to 2007, as well as annual patch fidelity for both juvenile and adult frogs.

Adult Movement Rates

Most daily movements were short and localized around immediate habitat features (Figure 14). Daily movement rates of adult male (n = 35) and female frogs (n = 51) did not differ significantly ANOVA (F = 0.31, P = 0.74). However, movement rates of both sexes combined differed by season (F = 4.07, P = 0.02), with daily rates significantly higher in the spring (mean: 9.9 ± 1.3 m) than in the fall (mean; 4 ± 1.8 m). Summer movement rates of adults (mean: 6.9 ± 1.3 m) were not significantly different from the spring or fall (Tukey Kramer multiple comparisons test).

Most radio tracked individuals completed at least one long-distance migration between two habitat patches. We calculated movement rates for eight radio tagged frogs that exhibited 10 seasonal migrations from 114 to 334 m between habitat patches. Most migrations were rapid (3.9 to 15.3 m/hour within 24 hours. The fastest overall movement rate observed was 30.3 m/ hour within a 1.75 hour period. However, Figure 14 shows two frogs (#8 and #13) which took up to five days to move overland between patches during the spring. Two of the 10 migrations were observed between 20:00 and 10:00, suggesting these frogs conducted their migrations at night. Furthermore, both of these migrations occurred overland during August, showing Cascades frogs will make rapid movements over dry land during dry periods. The fastest long-range movement rate (> 500 m) detected was an adult male that traveled from DPM to ECH, a minimum distance of 839 m, with a 238 m elevation gain, in less than 4.6 days (Figure 15A, #7). This dispersal event was determined from a mark-recapture basin census, so the actual movement rate was likely underestimated.

Migration Routes

Examples of migration routes used by radioed Cascades frogs are displayed in Figure 14. Overall, Cascades frogs appeared to choose the shortest and most direct routes while moving within and between habitat patches in Echo Lake basin. Throughout the Cascades frog active period, many habitat patches were hydrologically connected through the basins expansive stream network. Many radioed frogs used these streams as corridors between habitats (e.g., Figure 14A, #6). However, overland migrations of radioed frogs were common, especially when patches were completely isolated or as stream corridors dried.

Overland routes sometimes occurred over difficult terrain with steep inclines. Two radioed frogs were found navigating through steep, to near vertical, terrestrial inclines during an August rain event in 2003. One individual (Figure14A, #6), climbed 20 m up a stream bank (70º slope) composed of bare soil and embedded boulders. This frog remained near the top of this

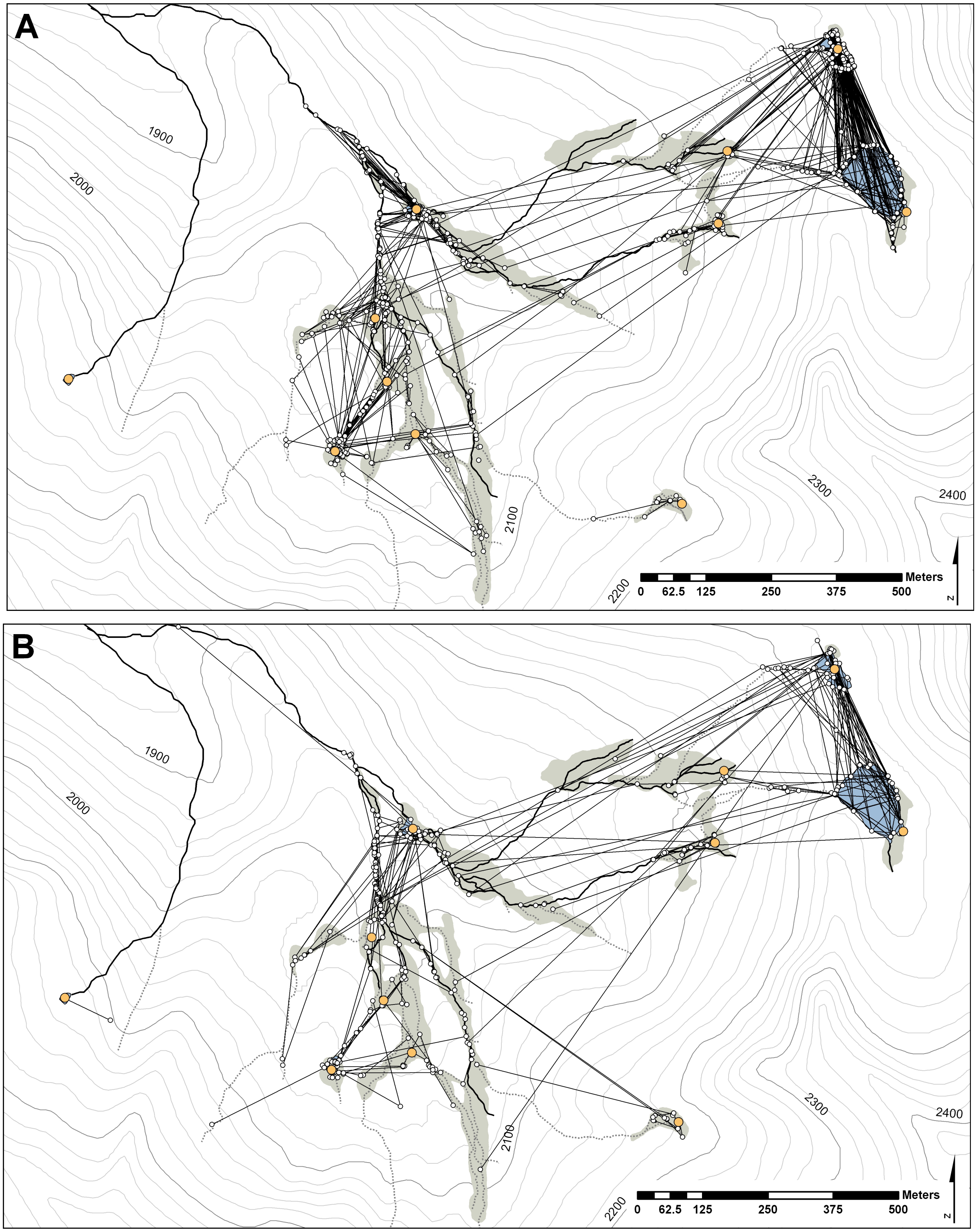


Figure 13. Maps of Echo Lake basin, Trinity Alps Wilderness, California, showing capture points (open circles) and connecting lines of 279 individual adult male (A) and 143 individual adult female (B) Cascades frogs captured two or more times from 2003 to 2006. Orange circles represent Cascades frog breeding sites used all five years of the study. Note that an individual frog can be represented by more than one line. Map properties follow those in Figure 2.

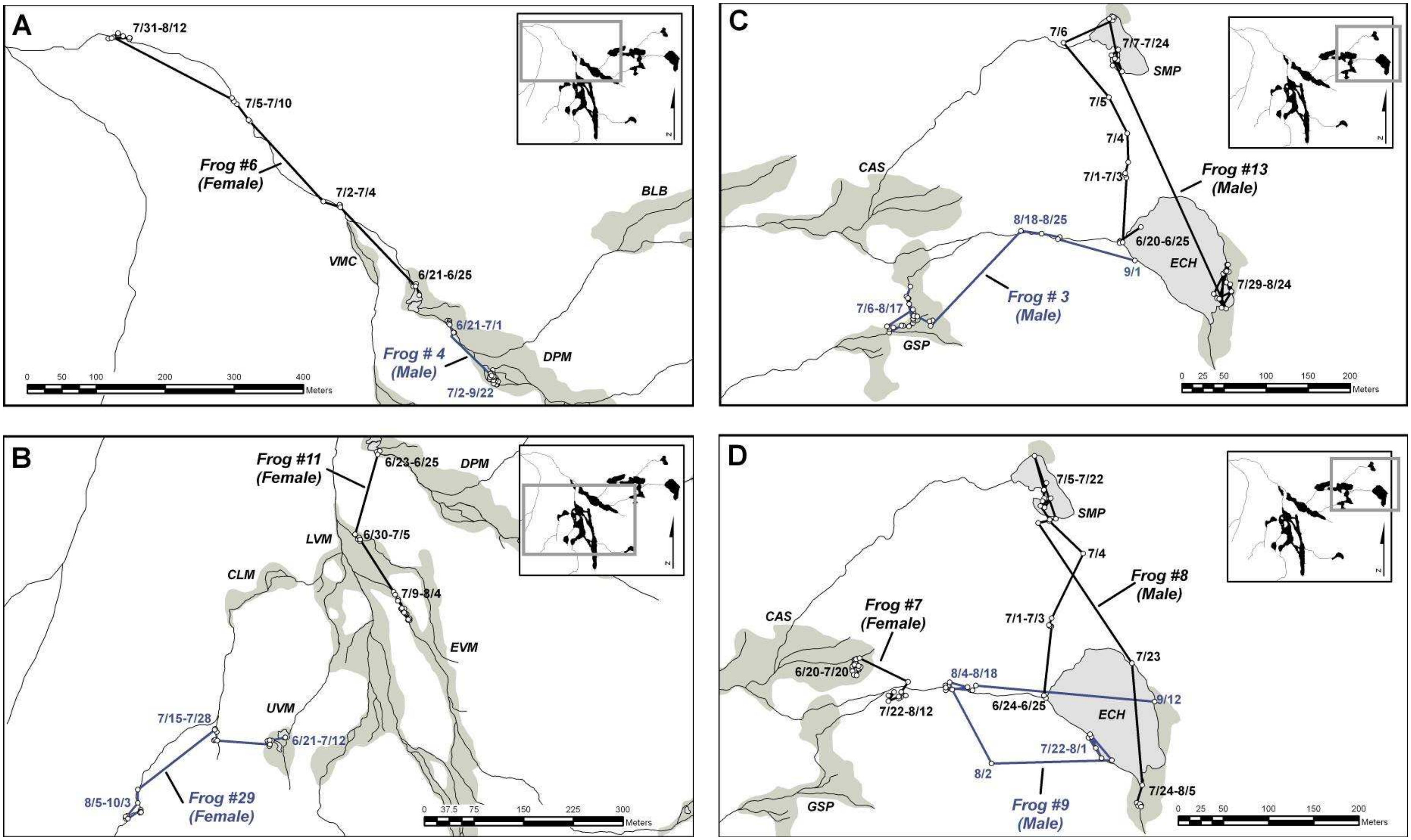


Figure 14. Examples of migration routes and timing of migration between seasonal resources for 9 telemetered Cascades frogs during the summers of 2003 and 2004 in Echo Lake basin, Trinity Alps Wilderness, California. Box detail in map inset represents the area within Echo Lake basin that is displayed. Map properties follow those in Figure 2.

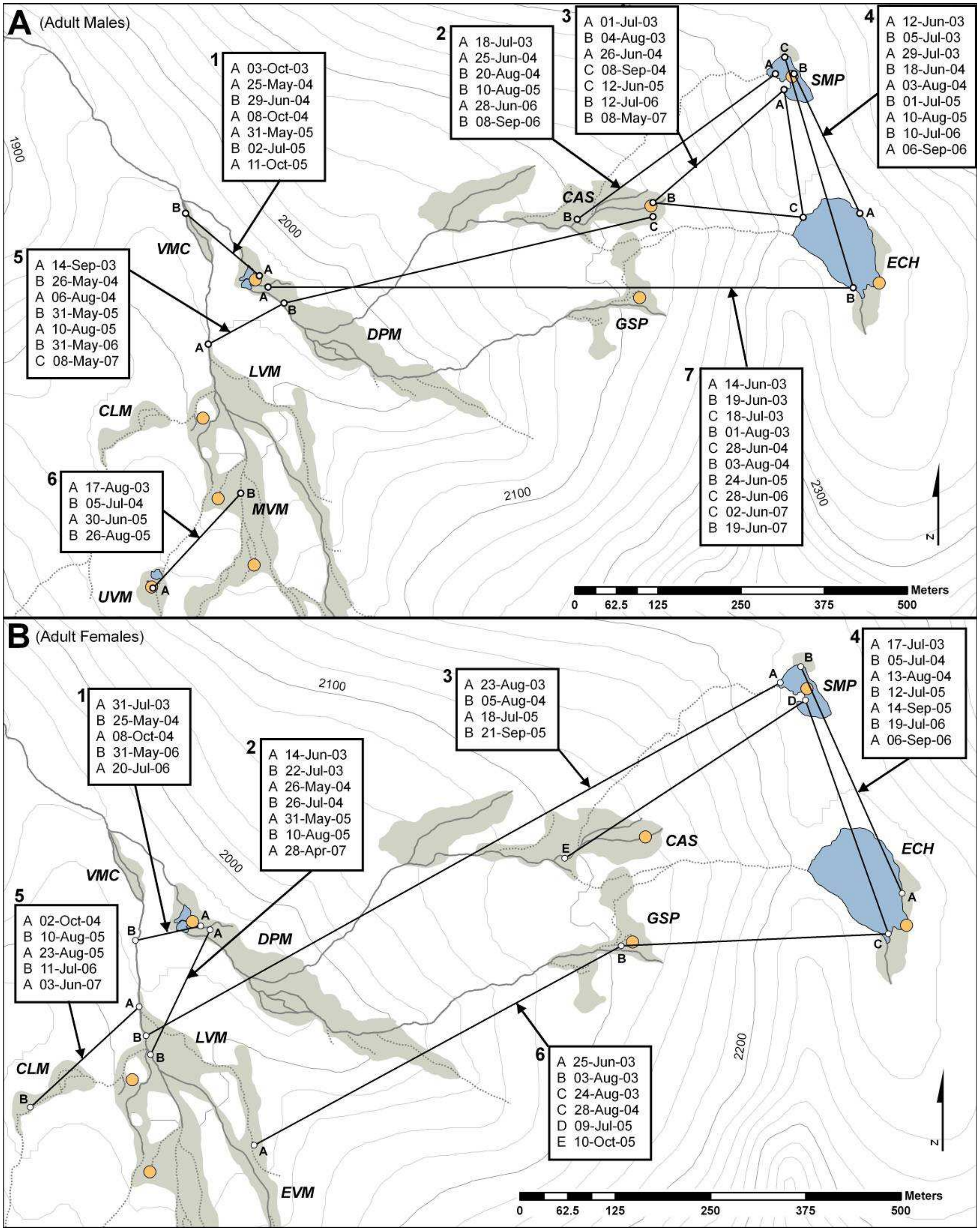


Figure 15. Examples of long-term annual migration patterns for seven adult male (A) and six adult female (B) Cascades frogs in Echo Lake basin, Trinity Alps Wilderness, California, from 2003 to 2007. All subsequent capture locations of individuals at specific habitat patches were within 25 m of original capture locations. Orange circles represent breeding locations used all four years. Map properties follow those in Figure 2.

bank within a rodent burrow for three days prior to returning to the stream directly below. Another individual (Figure14D, #9), navigated 220 m overland which included a descent down a steep (> 70º slope) couloir in a rocky outcrop south of Echo Lake. This frog was found on 2 August perched midway up a near vertical cliff section approximately four meters high, and subsequently navigated down the following day.

Overland migrations usually shortened the distance and elevation gradients traveled between patches considerably. For example, the stream distance between ECH and SMP is 760 m, whereas the overland distance is ~250 m. Furthermore, if individuals were to use the stream route to migrate between these sites it would require a steep decent of 112 m followed by a steep 125 m climb. In the early spring the outlets of both sites, as well as the rocky knoll separating them, are completely snow-covered with depths reaching up to 3.5 m. Through telemetry, we determined Cascades frogs migrated prior to breeding between these patches in deep snowpack along a narrow snowmelt crack between a rock outcrop and snowfield (< 1.5 m wide) (Figure 14D, #8). The extent to which frogs migrated overland between ECH and SMP is evident in Figure 13 where at least 161 round-trip migrations occurred from 2003 to 2007.

Seasonal Migrations of Adults

Many adult frogs completed seasonal migrations (> 100 m) between breeding, summer and wintering habitats (Figure 13 and 15). Of the frogs that migrated (n = 315), distances traveled to breeding habitats were significantly greater (mean: 319 ± 19 m) than those to wintering habitats (mean: 231 ± 17 m) (Kruskal-Wallis one way ANOVA on ranks test: H = 19.8, $P < 0.001$). In contrast, migration distances traveled to summer habitats (mean: 251 ± 11 m) were not significantly different from those to breeding or over-wintering areas (Kruskal-Wallis Z-test, Bonferroni correction: $Z = 2.39$).

Breeding Migrations

During the breeding season, most adult Cascades frog captures were narrowly distributed and highly concentrated around breeding sites. Many of these individuals wintered within, or in close proximity (< 100 m), to breeding habitats (n = 76). However, almost half (47% of females and 45% of males) completed spring migrations (> 100 m) each year directly after spring emergence between separate wintering and breeding habitat patches (Figure 16). Of the frogs that migrated, females moved significantly farther than males to reach breeding areas (Mann-Whitney U test: $Z = 2.84$, $P = 0.004$). Females moved up to 1001 m (mean: 491 ± 79 m), while males moved up to 844 m (mean: 266 ± 17 m).

The largest round-trip migration observed for an adult female between breeding and wintering habitats was 1980 m (Figure 15B, #3). This female wintered in a stream 239 m below her breeding site on the opposite side of the basin for two consecutive years. Remarkably, all other established breeding sites in the basin were closer to where this frog wintered than where she chose to breed. This demonstrates that some frogs will overlook much closer available breeding locations to reach specific, possibly natal breeding areas up to one kilometer away.

The farthest round-trip migration completed by a male between breeding and wintering habitats was 1607 m (Figure 15A, #7). This male was captured at an active breeding site (DPM) in the spring of 2003. Five days later this male was recaptured at Echo Lake, a distance of 886 m and 240 m elevation above his first capture point. Remarkably, this rapid movement was completed when most of the basin was covered in deep snow and the steep outlet of Echo Lake

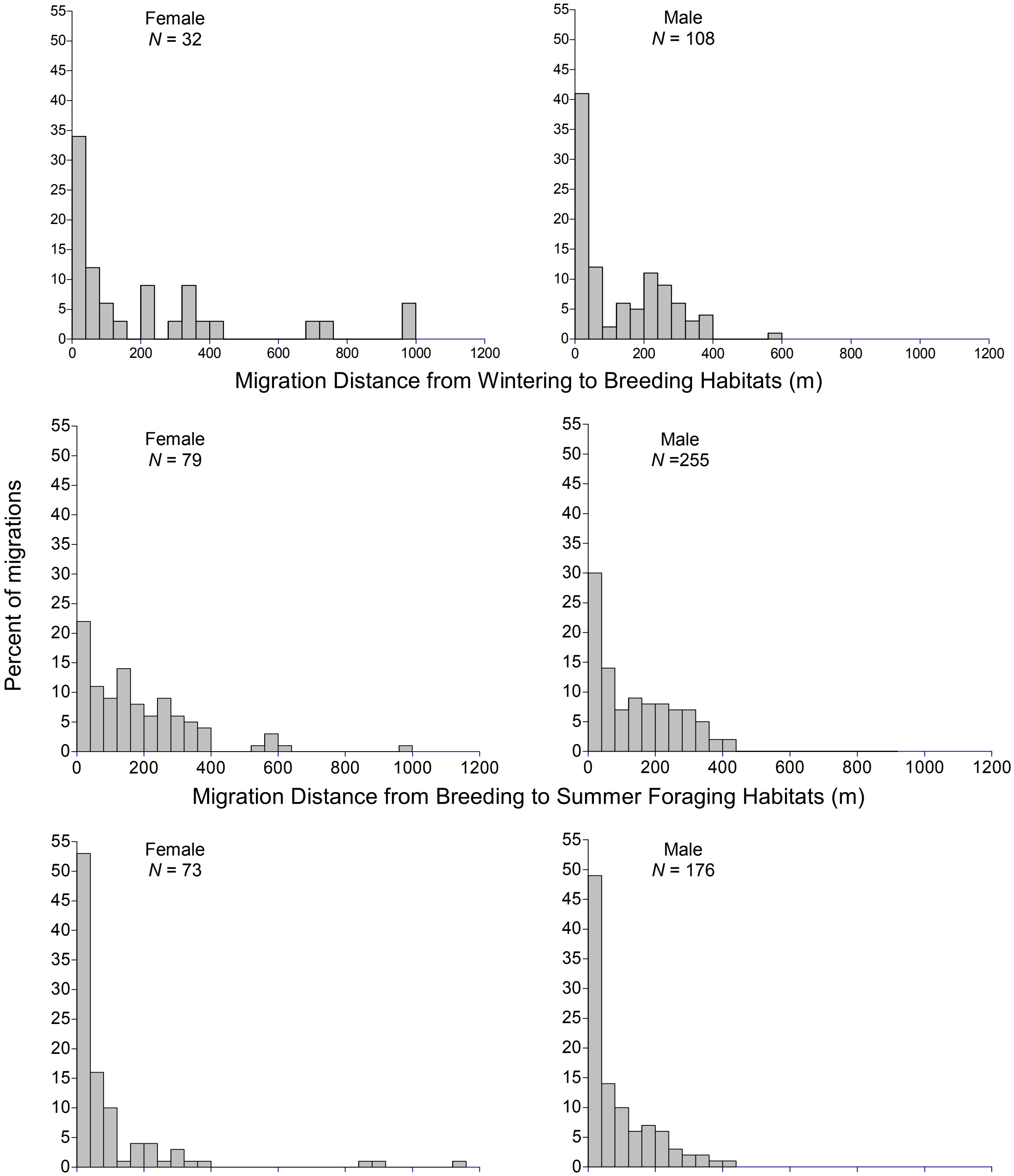


Figure 16. Frequency of migration distances traveled by adult female (left column) and adult male (right column) Cascades frogs between breeding, summer and winter seasons from 2003 to 2007 in Echo Lake basin, Trinity Alps Wilderness, California. Each migration represents a movement that occurred between two successive seasons for each annual activity cycle. Bar widths represent 40 meter bins. Individual frogs may have been counted more than once between different years.

was completely covered by snow for 250 m. This male was then recaptured 30 days later at SMP during intense breeding activity. Shortly after this, the male was again captured at Echo Lake where he over-wintered. In 2007, another adult male moved between two active breeding sites (CAS to SMP) within 19 days. This male was captured at CAS during active breeding activity on 8 May and then 19 days later at SMP, during active breeding activity. These movement patterns clearly demonstrate multiple breeding sites, up to 1 km away, can be used by individual male frogs during the same breeding season by moving to new breeding sites as snow melts at various elevations.

Summer Migrations

During the summer, Cascades frogs were widespread and occupied the greatest area and variety of habitats in Echo Lake basin. Many adult frogs completed migrations (> 100m) directly after breeding to other areas for summer foraging. Only 40% of females ($n = 32$) and 50% of males ($n = 127$) were captured within 100 m of their spring breeding habitats during the summer. Of the frogs that migrated, there was no significant difference between adult males and female migration distances (Mann-Whitney U test: $Z = 0.48$, $P = 0.63$). Females ($n = 47$) moved up to 989 m (mean: 279 ± 24 m), while males ($n = 128$) moved up to 591 m (mean: 241 ± 8 m) to reach summer habitats (Figure 16). During, and directly after, the breeding season, much of Echo Lake basin remained saturated from receding snowpack, so soils remained damp and most streams were still flowing. Based on these conditions, and radio telemetry results, it appeared frogs were least restricted in moving to other patches during this time. For example, six individuals (Figure 14, # 4, 6, 8, 11, 13 and 29) demonstrated rapid migrations from breeding sites directly after breeding subsided.

Winter Migrations

By the fall, the majority of adult frogs (73% of females [$n = 53$] and 68% of males [$n = 120$]) were captured within 100m of their summer locations, suggesting many summer habitats away from breeding sites were suitable and used for over-wintering. However, many habitats dried up as the fall approached, causing frogs to move to areas with sufficient water for over-wintering. Of the frogs that migrated from summer to winter habitats (> 100 m), there was no significant difference in distance moved between males and females (Mann-Whitney U test: $Z = 0.93$, $P = 0.35$). Migrating females ($n = 20$) moved up to 1158m (mean: 317 ± 67 m) while migrating males ($n = 56$) moved up to 427m (mean: 200 ± 10 m) to reach over-wintering habitats (Figure 16).

Inter-Annual Adult Migration Patterns

During this study, many adult Cascades frogs exhibited strong migration patterns between seasonal resources throughout Echo Lake basin. Furthermore, many individuals repeated similar migration patterns between patches for multiple years. Figure 15 demonstrates some examples of these patterns by both adult male and female frogs. These frogs completed similar annual migration patterns for up to five years. Based on recapture success, the best case example of annual migratory patterns was between ECH and SMP. This pattern is apparent because SMP dried completely by late summer (Figure 3), which forced frogs to find permanent water-bodies for over-wintering. ECH had the strongest influence on SMP with 75% of all adult SMP captures derived from ECH. The remaining 25% of adult SMP captures came from patches further away and from lower elevations. Although ECH and SMP are in close proximity (~250 m round-trip), the majority of the distance between the two sites is over land that traverses a rugged, rocky knoll. During the early spring, adult frogs migrated overland from ECH to SMP prior to breeding (Figure 7, C and D). Most frogs returned to ECH directly after the breeding season for summer foraging and over-wintering. Ninety out of 156 (58%) individual adults captured at ECH completed at least one round-trip breeding migration between these patches. Of the frogs that migrated, at least 48% completed annual migrations twice, 21% three times, and 9% four times. Only one adult male frog (~1%) was detected to complete this annual migration for five straight years (Figure 15A, #7). We suspect, based on passive mark-recapture sampling, these are minimum estimates of inter-annual migration patterns between two isolated patches.

Although many frogs exhibited consistent breeding migration patterns between specific patches, variation in annual migration strategies for frogs with long capture histories was also apparent. Based on capture histories of 34 gravid adult females in amplexus, we captured one in amplexus at SMP in 2003 and then again in amplexus at ECH in 2004. We also found five male frogs had stayed at ECH during an entire year but had completed breeding migrations to SMP in prior and subsequent years. These males were all captured at the ECH during the breeding season, and were actively engaged in breeding activities when we would have expected them to be breeding at SMP. Alternatively, another adult male frog (Figure 15A, #5) exhibited a strict migration pattern between DPM and LVM for three straight years. During the breeding season in the following year this male dispersed to CAS, a different breeding site 570 m away from his previous breeding site. Finally, a few frogs showed a nomadic distribution, with no apparent migration pattern between years. For example, an adult female (Figure 15B, #6) moved between five different habitat patches over three years, all of which contained active breeding sites. A male frog (Figure 15A, #3) also had a nomadic distribution and visited three different sites over four years. These irregular migration patterns are evidence that some adult frogs choose to breed at different sites in different years.

Immature Age Classes Movements and Dispersal

Unlike adults, YOPY and juvenile Cascades frogs did not have reproductive behavior as part of their annual life history. Although the breeding season had profound annual and seasonal effects on adult spatial patterns, immature age classes of Cascades frogs displayed remarkably different spatial and movement patterns than adults. This section summarizes movements of immature age classes over the course of the study.

Young of Previous Year Movements

The YOPY age class of Cascades frog's had distinct spatial patterns that differed from all other age classes. Most YOPY were captured in association with breeding sites. For example, 69% of YOPY captures were within 25 m, followed by 94% within 100 m of breeding sites (Figure 17). The furthest capture of a YOPY away from a breeding site was 312 m. Because YOPY were marked with a batch VIE mark, we could only determine dispersal behavior for a limited number of individuals. We captured at least nine unique YOPY out of 544 marked individuals that dispersed distances greater than 100 m between two or more habitat patches within the same year. These individuals moved at least 130 to 439 m (mean: 238 ± 38 m) between habitat patches. Based on these results, it appears this age class has strong fidelity to natal sites with only a few moving away from breeding areas their first year after metamorphosis.

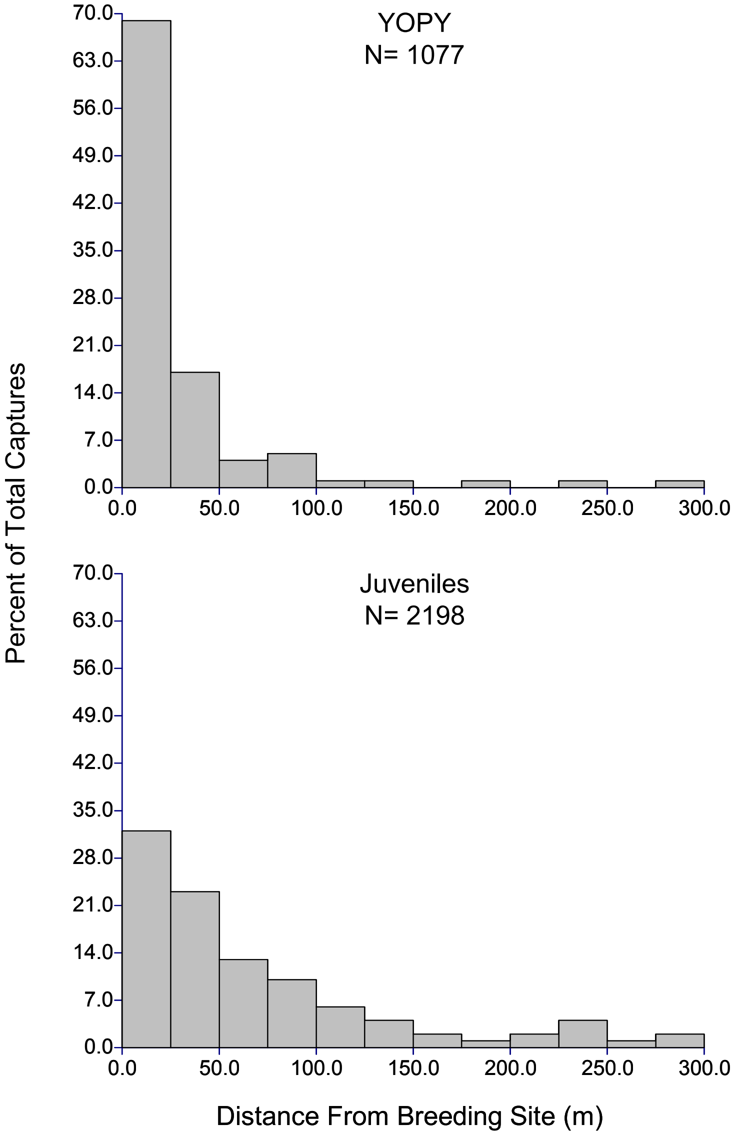


Figure 17. Percent of all immature Cascades frog captures, separated by age class, that were captured at various distances (25 meter bins) from breeding sites in Echo Lake basin, Trinity Alps Wilderness, California. YOPY captures represent years 2003 through 2005, juvenile captures represent years 2003 through 2006.

Juvenile Dispersal

In contrast to YOPY, juvenile Cascades frog captures were distributed farther away from breeding sites. Only 31% of juveniles were captured within 25 m of a breeding site and 78% within 100 m (Figure 17). Juvenile frogs were found using a variety of habitats, especially streams and ephemeral sites (Table 3, Figure 10). However, unlike adults, juvenile frogs did not display distinct seasonal or annual migration patterns, but moved more in a random diffused manner. Most noticeably, unlike adult movement patterns (Figure 13), dispersal paths of juvenile frogs were less centered around breeding locations (Figure 18). Of the 540 juvenile frogs captured more than once between the years of 2003 and 2006, 55% dispersed greater than 100 m from their original locations (Figures 18 and 19). The mean net dispersal distance for juvenile frogs that moved greater than 100 m was 338 ± 12.5 m (n = 296). Furthermore, of the 121 juvenile frogs that had three years between locations, 70% had net dispersal distances greater than 100 m. The mean net dispersal for this group of juveniles was 447 ± 29.2 m. Finally, 53 juvenile frogs dispersed greater than 500 m, and seven dispersed distances greater than 1000 m. Maximum net dispersal distance for a juvenile frog within Echo Lake basin was 1171 m.

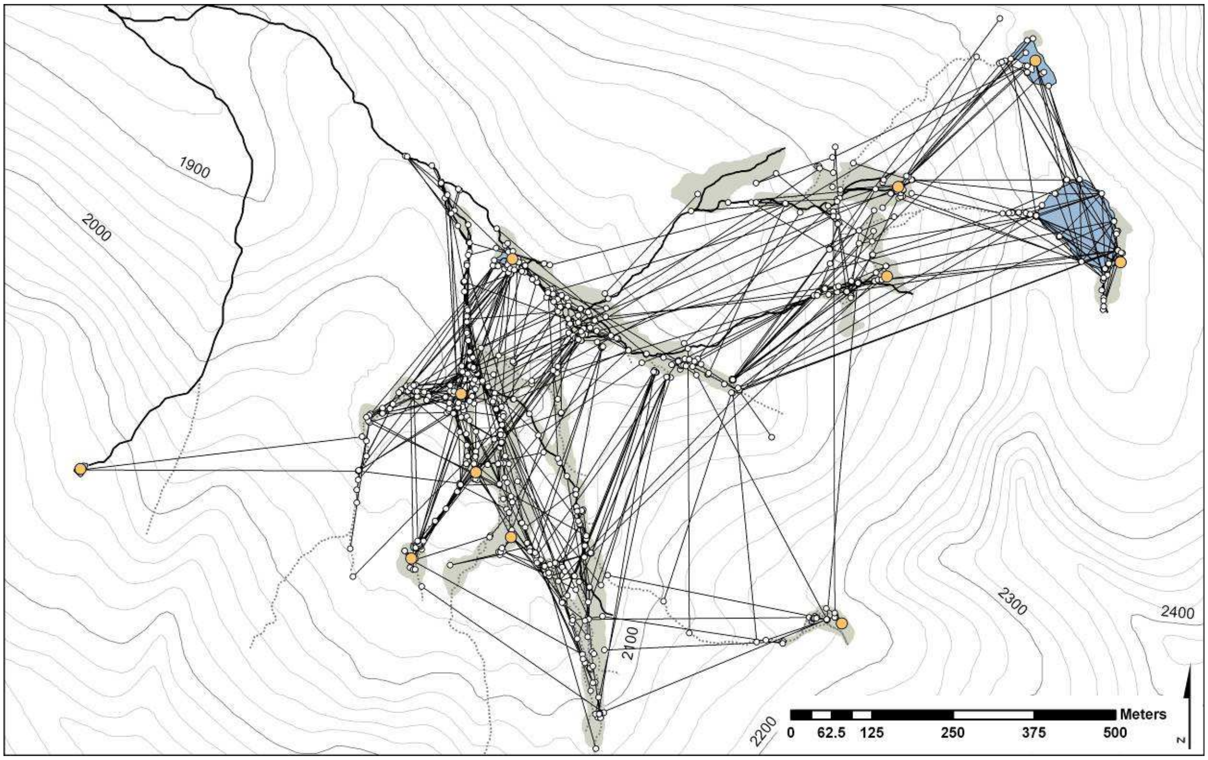


Figure 18. Map of upper Echo Lake basin, Trinity Alps Wilderness, California, showing capture points (open circles) and connecting lines of 471 individual juvenile Cascades frogs captured two or more times from 2003 to 2006. Orange circles represent breeding sites used by Cascades frogs for all five years of the study. Note that an individual frog can be represented by more than one line. Map properties follow those in Figure 2.

Inter-basin Dispersal

Perhaps the most unexpected movement information gathered from this study was the dispersal of individual Cascades frogs between neighboring basins. We documented inter-basin dispersal of 17 individual frogs that were recaptured in one of four neighboring basins (Stony Creek, Echo, Siligo and Deer basins) (Figure 20, Table 4). Minimum air distances traveled by these individuals between successive captures ranged from 769 to 1558 m. The majority of distances traveled were over steep and rocky terrain lacking permanent aquatic features, with at least 12 individuals moving greater than 500 m over land. Although dispersal movements of these frogs occurred between 03 July and 14 September, the shortest travel time captured was a

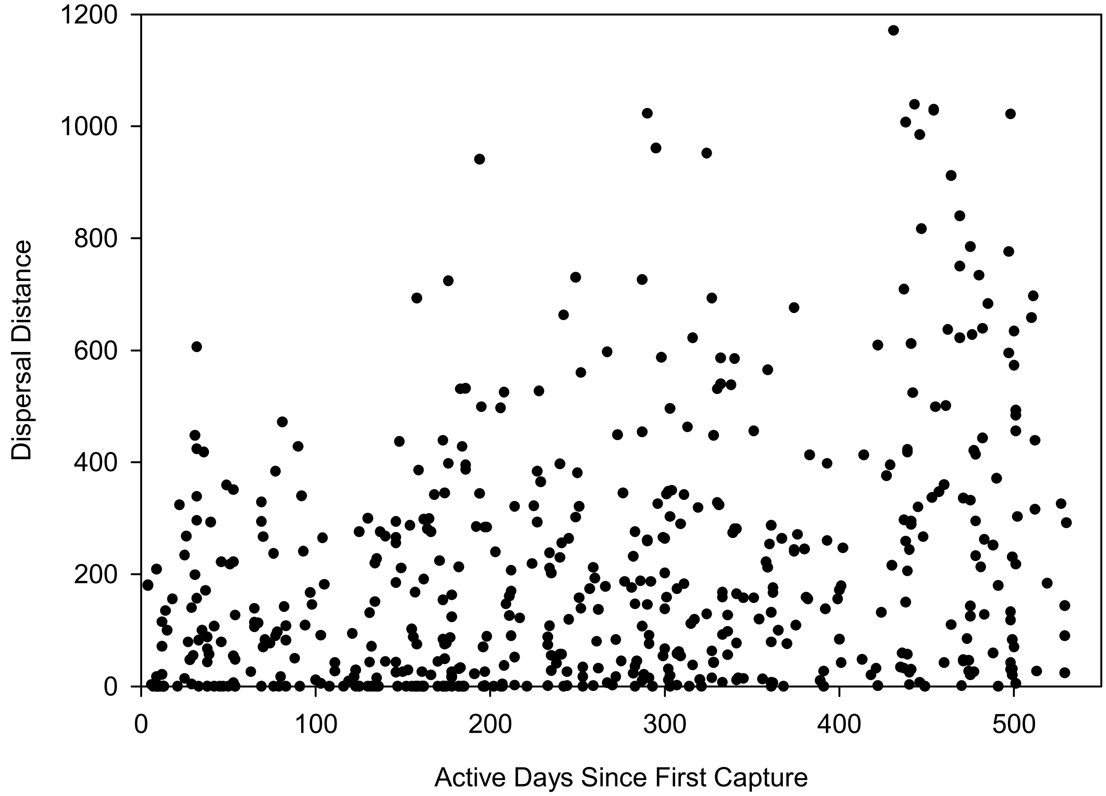


Figure 19. Net dispersal distance for 540 juvenile Cascades frogs captured two or more times in Echo Lake basin, Trinity Alps Wilderness, California, from 2003 to 2006. All distances were determined as the minimum air distance between the first and final captures of each individual frog. Inactive days (winters) were omitted from the total days between captures since no movements were assumed during winter dormancy.

movement within 19 days (03 July and 22 July). This movement is evidence that inter-basin movements may have been facilitated in early to mid-summer when the ground was still saturated from snowmelt. Routes most likely followed low points in saddles associated with mountain passes and avoided steep jagged ridges and peaks (Figure 20).

Final capture locations of inter-basin dispersing frogs were higher in elevation (paired *t*: $t = -1.86$, $P = 0.04$) than initial capture locations suggesting a positive bias in elevation with dispersal. The maximum vertical gain was 308 m from a frog that left lower Siligo basin and climbed up to Echo Lake, the second highest habitat patch in Echo Lake basin. A minimum of eight individuals dispersed as juveniles and three as adults. The remaining six frogs grew from juveniles to adults between captures, so age class could not be determined during the actual movement event. Sex ratios of the frogs ($n = 17$) were equal (8 females, 8 males, 1 unknown) suggesting unbiased gender dispersal. Destinations for 15 out of 17 animals were within 50 m of traditional Cascades frog breeding sites (Figure 20) which indicates a high potential for inter-basin gene flow. Although we could not determine if these dispersal events resulted in successful reproduction, potential gene flow from these animals via “leapfrogging” spanned an air distance of 5.2 km overall (Figure 20).

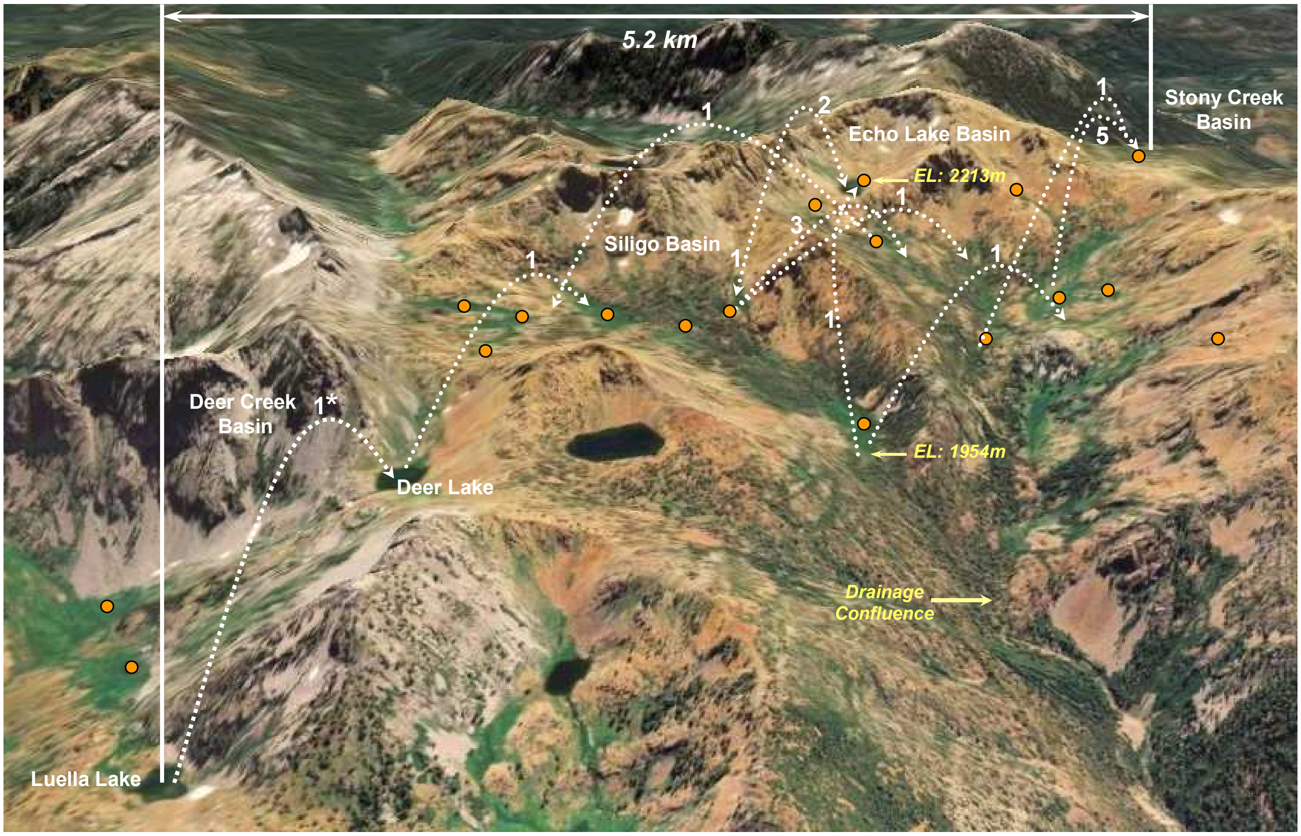


Figure 20. Connecting lines of seventeen individual Cascades frogs that dispersed between four neighboring watersheds in the southeast Trinity Alps Wilderness, California. Arrows at the end of dotted lines represent movement direction. Numbers above connecting lines represent the number of individuals that moved a particular pattern. Orange circles represent traditional breeding sites used by Cascades frogs throughout the study period. The overall air distance linking habitat patches across the landscape via dispersal was 5.2km, which represents the minimum potential gene flow in this landscape.

**frog did not move between a pass or major drainage, but this movement adds to overall potential gene flow through patch connectivity, (K. Pope, unpubl. data, USFS/ UC Davis).*

Table 4. Summary of dispersal movements from 2003 to 2007 for 17 individual Cascades frogs captured in adjacent watersheds from where originally marked in the southeast Trinity Alps Wilderness, California.

frog ID	Sex	Start/End SUL (mm)	Initial Capture Date	Recovery Date	Basin Movement Direction	Days Between Captures[a]	Stream Dist. (m)[b]	Min Dist. (m)[c]	Start Elev. (m)[d]	Max Elev. (m)[e]	End Elev. (m)[f]	Max Change (m)[g]	Net Elev. (m)[h]
395B	F	47/ 48	7/3/2004	7/22/2004	Echo to Stony	19	28645	1087	2035	2243	2127	208	92
6467	F	< 40/ 46	6/25/2003	6/17/2004	Echo to RMM	358*	28660	1143	2034	2243	2117	209	83
481F	F	– / 54	7/9/2005	7/12/2006	Siligo to Echo	368	3636	931	2130	2262	2093	132	-37
1368	F	43/ 53	5/26/2004	7/19/2005	Echo to Siligo	418	4137	1558	2091	2262	2180	171	89
2137	F	– / 46	7/9/2005	10/6/2006	Siligo to Echo	450	3773	769	2135	2262	2115	147	-20
1020	F	41/ 63	6/10/2003	10/9/2004	Siligo to Echo	487	3063	1505	1954	2262	2213	308	259
0A64	F	57/ 64	7/23/2004	6/2/2007	Echo to Siligo	1044	4094	883	2213	2262	2129	133	-84
8186	F	< 40 / 41	7/9/2005	6/9/2007	Siligo to Echo	700	3505	1074	2132	2262	2013	130	-119
0C71	M	– / 55	7/9/2005	8/10/2005	Siligo to Echo	32	4241	734	2130	2262	2224	132	94
5643	M	– / 44	7/9/2005	8/30/2005	Siligo to Echo	52	4134	968	2135	2262	2213	127	78
2C1F	M	51/ 55	9/4/2004	8/22/2005	Echo to RMM	351	28846	978	2075	2243	2124	168	49
2462	M	47/ 57	7/15/2005	5/8/2007	Echo to RMM	662	28867	945	2078	2243	2119	165	41
6C33	M	< 40/ 56	7/10/2003	6/29/2005	Echo to RMM	719*	28987	823	2113	2243	2116	130	3
9912	M	64/ 67	7/15/2003	7/11/2005	Deer to Siligo	726	21890	1229	2173	2306	2148	133	-25
7A43	M	59/ 66	6/11/2003	7/28/2005	Siligo to Echo	777	2511	1218	1957	2017	2017	60	60
5C69	M	41/ 63	7/24/2003	5/8/2007	Echo to RMM	1383	28240	1534	1975	2243	2119	268	144
0A11	U	– / 43	7/9/2005	9/14/2005	Siligo to Echo	67	3786	806	2133	2262	2117	129	-16
Mean (SE)						507 (± 90)	13589 (± 2985)	1070 (± 64)	2088 (± 18)	2243 (± 15)	2128 (± 14)	162 (± 14)	41 (± 22)

*[a] Duration between captures, *recapture of an individual with only a VIE site/year batch mark; initial capture date was determined as the first day VIE was used at the initial capture site to avoid biasing movement to the shortest time intervals. [b] Minimum stream distance in meters between initial and final captures. [c] Minimum straight-line distance moved between initial and final capture locations. [d] Elevation in meters at initial capture location. [e] Lowest elevation at ridge saddles separating two adjacent basins. [f] Elevation in meters at final capture location. [g] Maximum elevation difference between the lowest and highest points. [h] Net elevation change between initial and final capture location.*

Patch Fidelity

A proportion of adult Cascades frogs showed seasonal and annual patch fidelity and did not migrate between patches within or between years. Furthermore, most adults that underwent seasonal migrations showed strong fidelity to one or more specific patches annually. Based on these two patterns, adult frogs exhibited strong annual patch fidelity. For example, 78% of adults exhibited annual patch fidelity from one year to the next (Table 5, Figure 21; 1 year) and 83% of adults captured in 2003 were recaptured within with same patch in 2006 (Table 5; 3 years). However, this slight increase in patch fidelity was insignificant ($\chi^2 = 0.27$,df = 1 $P = 0.61$). Within adults, females exhibited the highest site fidelity, with 79% of females captured in the same patch from one year to the next (Table 5, Figure 21; 1 year) and 91% of females captured and recaptured in the same patch in 2003 and 2006 (Table 5, Figure 21; 3 years).

Table 5. Summary of Cascades frogs that exhibited annual site fidelity to specific patches within Echo Lake basin, Trinity Alps Wilderness, California, between one, two and three years.

	1 Year			2 Years			3 Years		
	N	# Fidelity	% Fidelity	N	# Fidelity	% Fidelity	N	# Fidelity	% Fidelity
Juveniles									
Female	176	105	59.7	135	58	43.0	48	16	33.3
Male	177	124	70.1	122	62	50.8	74	31	41.9
Totals:	353	229	64.9	257	120	46.7	122	47	38.5
Adults									
Female	66	52	78.8	34	29	85.3	11	10	90.9
Male	175	137	78.3	101	72	71.3	31	25	80.6
Totals:	241	189	78.4	135	101	74.8	42	35	83.3
All	594	418	70.4	392	221	56.4	164	82	50.0

Juveniles showed a significant decrease in annual patch fidelity over time ($\chi^2 = 24.8$, df = 1, $P = < 0.01$, Table 5, Figure 21). Sixty-four percent of juveniles exhibited annual patch fidelity from one year to the next (Table 5, Figure 21; 1 year), whereas only 38% were captured within a specific patch in 2003 and recaptured within with same patch in 2006 (Table 5, Figure 21; 3 years). Patch fidelity by juvenile males decreased over time, with 70% of juvenile males having patch fidelity from one year to the next, but only 42% captured and recaptured in the same patch in 2003 and 2006. Juvenile females had the lowest annual patch fidelity, with 59% having fidelity to a patch from one year to the next and 33% captured and recaptured in the same patch in 2003 and 2006. The difference between adult and juvenile patch fidelity indicates that juveniles are the primary dispersers in this population, likely exhibiting relatively low philopatry to natal sites as they mature to adults. In contrast, adult frogs show strong annual fidelity to specific habitats, even when they seasonally migrate between patches.

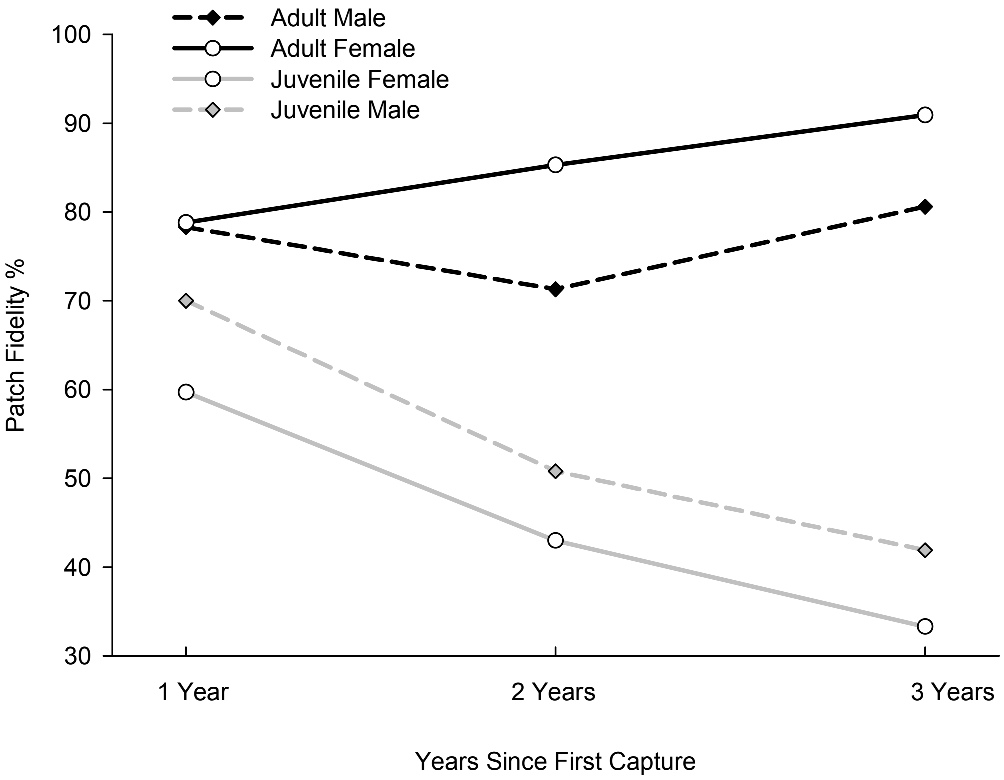


Figure 21. Proportion of individual Cascades frogs, separated by age class and gender, that exhibited annual site fidelity to a specific habitat patch between one, two and three years in Echo Lake Basin, Trinity Alps Wilderness, California. Individual frogs were only included once within each time-elapsed category.

Breeding Ecology

Timing and Duration of Breeding

Breeding activity at individual sites within the basin was explosive with actual egg deposition occurring over a period less than 10 days. However, the overall duration of breeding activity throughout the entire basin was prolonged due to differences in individual site elevations, which ranged from 1976 to 2226 m. For example, duration of breeding averaged 58 ± 3.4 days basin-wide, ranging from 49 to 69 days over five years studied. Furthermore, annual variation in snow accumulation affected the initiation date and duration of breeding seasons. Onset of breeding activity occurred much later in heavy snow years. For example, we found initiation of annual oviposition to be highly dependent on annual snow accumulation at both low elevation (DPM; df = 3, $P = 0.02$, $R^2 = 0.88$) and high elevation (ECH; df = 3, $P = 0.04$, $R^2 = 0.92$) sites (Figure 22). At the lowest elevation site (DPM), the difference in breeding initiation date between the lightest (38%) and the heaviest (251%) years of snow accumulation was 43 days. There were only six days of overlap between these two breeding seasons (Figure 22).

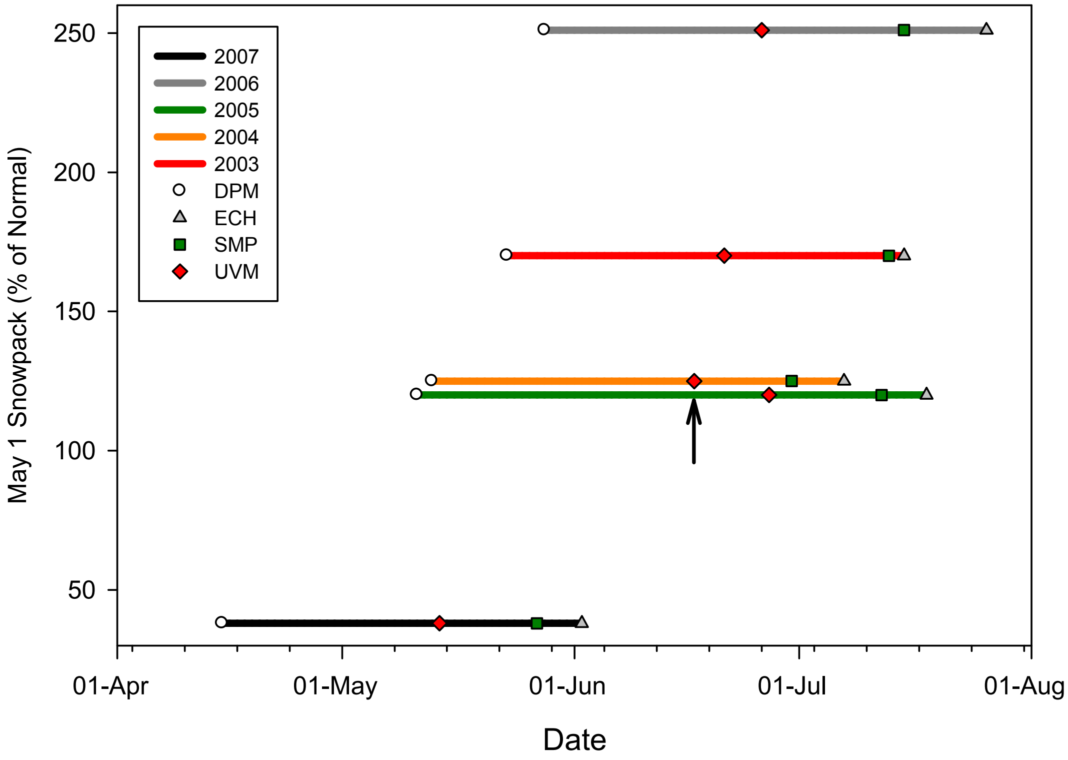


Figure 22. Breeding season timing and duration based on snowpack, for Cascades frogs at four sites with differing elevations in Upper Deep Creek Basin, Trinity Alps Wilderness, California, from 2003 to 2007. Bars extend from the beginning of oviposition at the lowest elevation site in the basin (DPM) to the end of oviposition at the highest elevation sites in the basin (SMP, ECH); UVM represents a mid-elevation site. The arrow on the 2005 bar represents the date of the only late snowfall event that occurred during the study, which delayed breeding at the mid- and high-elevation sites.

Although 2005 snowpack was only slightly above average (120%), a late snow storm in the middle of June effectively made it the longest breeding season over the five years. Snow, surface ice, and cold weather from this late storm were likely responsible for delaying reproduction at higher elevation sites. The 2005 breeding season lasted 13 days longer than the 2004 season (125% snowpack) and 20 days longer than 2007 (38% snowpack), the shortest breeding season (see arrow in Figure 22). Timing in reproduction may have also been influenced by water temperature. For example, at SMP from 2003 through 2007, eggs were not deposited until water temperatures reached a minimum of 7ºC, even though sufficient shoreline and pond surface area was available (snow and ice free). This minimum temperature threshold was slightly higher than the 6ºC minimum observed by Sype (1975) and similar to the 7.1ºC minimum observed by Briggs (1987).

Annual Egg Mass Production

We observed a total of 275 individual Cascades frog egg masses from 2003 to 2007 in Echo Lake basin (Table 2). From 2003 to 2006, reproductive output was similar, with a mean of 49 (range 46-53) egg masses observed annually. During the 2007 breeding season, we observed

80 egg masses, a 63% increase in production compared to the previous four-year average. At the patch level, SMP and DPM produced the most egg masses annually, with each accounting for 21% (42% combined) of the five-year total. UVM and Echo Lake accounted for 15% and 8%, respectively, of the five-year total.

Larval Stage Development

Like oviposition, the duration of Cascades frogs larval stage varied by site and year. We did not find any evidence of over-wintering tadpoles over the length of this study. In 2007, when snowpack was 38% of normal, we found frogs metamorphosing as early as 02 August. In contrast, during our last survey in 2006, when snowpack was 251% of normal, we observed tadpoles at six sites on 08 October. On this date, we observed tadpoles in three ponds at PTH and at Echo Lake with Gosner stages ranging from 34-39, which are prior to front leg emergence (Gosner 1960). Based on these Gosner stages, and fall water temperatures, it's highly unlikely tadpoles successfully metamorphosed at these sites. We conducted dip net surveys in the spring of 2007 and failed to detect successful over-wintering of tadpoles at these sites. Furthermore, in 2007, we failed to find any YOPY individuals at Echo Lake, and only saw a maximum of two YOPY individuals during a survey at PTH in the 10 surveys conducted at that site. A similar pattern occurred in 2005, with only 120% snowpack, when a late snowstorm caused higher elevation breeding sites to have delayed availability. On 10 October, we found metamorphosed frogs at lower elevation sites, but found tadpoles at four of the high elevation sites. The longest larval period we observed was in 2005 at a cold spring pond in DPM. Three egg masses were deposited in this pond between 21 and 30 May. We still observed tadpoles in this pond on 11 October which represented a minimum of a four-month larval period.

Cascades frog Mortality and Abnormalities

Mortality and Predation

Cascades frog mortalities were uncommonly observed. No mass mortality or large winter kill events of post-metamorphic Cascades frogs were detected during this study. However, winter kill rates may be hard to detect because Cascades frogs tend to bury themselves into substrates during winter months making observations of mortalities difficult (Briggs 1987). Winter kill, caused by depletion of oxygen in waterbodies, can be common for Mountain Yellow-Legged frogs (Bradford 1983), a close relative to the Cascades frog which occupies similar high-elevation environments. A total of 17 Cascades frog mortalities (14 adults and three juveniles), not attributable to predation, were observed during the study. Nine of these mortalities were observed during the early spring and appear to be from winter kill, with three dead adults observed at one pond during the same survey. Of the other non-predator mortalities observed during the early spring; a pair of adults were found dead in amplexus after a late spring freeze, an adult female was found dead at a breeding site after she oviposited her eggs and one adult female was found dead in a stream with a leg entrapped in a small bedrock crevasse.

Although infrequent, egg masses, tadpoles and recently metamorphosed frogs suffered mortality from desiccation as ponds dried. Three egg masses out of 275 (~1%) suffered mortality from desiccation, all due to being placed in shallow alcoves that dried rapidly as snowmelt subsided and pond elevations dropped. One egg mass became displaced into a temporary stream, hatched out, and the tadpoles subsequently died due to the stream drying up (Garwood et al.

2007). A minimum of 23 (8.4%) egg masses were found to be infected with a *Saprolegnia* sp. fungus, with the proportion of eggs infected at detection ranging from one to 100 percent.

Each year SMP dried in October, causing mass mortality of Cascades frog tadpoles. In addition, newly metamorphosed Cascades frogs were forced to respond behaviorally (Figure 5). During this period, we frequently observed hundreds of recently metamorphosed frogs taking refuge in mud cracks and under boulders and wood debris piles around the dried pond. On 07 October 2007, over 100 emaciated metamorphosed Cascades frogs were observed at SMP which had been dry for exactly one month (31 days). SMP is greater than 200 m from the nearest water and is suspected to be a major source of fall mortality for newly metamorphosed frogs based on poor site recruitment. For example, over five years, this site accounted for 21% of the total egg mass production of Echo Lake basin but no YOPY individuals were observed from this location.

Direct predation on Cascades frogs was not commonly observed, though it is suspected to be a major source of natural mortality for both tadpoles and frogs. A variety of predators including birds, snakes and invertebrate larvae were observed feeding on Cascades frogs. Of the adult Cascades frogs utilized for radio telemetry, 16% (eight of 50) frogs were eaten by garter snakes while carrying radio transmitters (five by common garter snakes, two by aquatic garter snakes and one unknown garter snake) (Garwood and Welsh 2005, and Appendix C). Both species of snake also consumed tadpoles as well as metamorphosed and juvenile Cascades frogs (see Section 7, Pope et al. *in review*). Clark's Nutcrackers and American Robins were observed feeding on both Cascades and Pacific treefrog tadpoles (Garwood 2006). J. Garwood also had multiple observations of American Dippers feeding on Cascades and Pacific treefrog tadpoles and newly metamorphosed individuals. A dragonfly larva (*Aeshna* sp.) was observed predating a newly metamorphosed Cascades frogs while it was alive (Garwood and Wheeler 2007). Potential predators not observed feeding directly on Cascades frogs but observed at, or had tracks around breeding ponds include: Spotted Sandpiper- commonly observed around many breeding ponds, Common Snipe- observed at one breeding pond, Great Blue Heron- one observed flying from a breeding area, Coyote- tracks observed for two years around a series of breeding ponds during the late summer, Black Bear- tracks common at two breeding ponds during the late summer and Shrews (*Sorex* sp.) - are common throughout the basin in meadow patches. Although not seen in this study, a mallard duck was observed eating a Cascades frog in the Trinity Alps at Tangle Blue lake in 2005 (Bernard Aguilar, DFG, pers comm.).

Abnormalities

Observed abnormalities of post-metamorphic Cascades frogs were relatively rare. From 2003 to 2006 we captured and marked 1669 individual Cascades frogs and found 58 individuals (48 juveniles, 10 adults) or 3.4% had various abnormalities. Observed abnormality rates from annual population captures averaged 1.2% (SE ± 0.23, range 0.68 to 1.65%). All abnormalities were observed in the limbs, with 88% restricted to the hind limbs. A total of 60% were derived from missing limbs (45% missing phalanges, 17% missing entire foot). Eighteen percent appeared to be wounds including swollen toes, open lacerations or exposed bone (phalanges). Ten percent appeared to be from previous broken leg and toe bones that subsequently healed. Two animals had leg bones of unequal length. Lastly, two animals had dislocated joints in one of the hind legs. Many Cascades frogs in the area breed in permanent spring fed ponds. These permanent ponds contain a variety of Dragonfly larvae (Anisoptera), a known predator of metamorphosing Cascades frogs (Garwood and Wheeler 2007). We have observed complete removal of limbs on metamorphosing Cascades frogs by Anisoptera suggesting they can be a major source of observed abnormalities in these ponds. Although we did not distinguish the cause of these abnormalities, which could either be malformations (developmental) or deformities (physical trauma), we suspect the majority of cases were caused by physical trauma from predation attempts. These observed abnormality rates are below 2% which is suggested as background levels for natural amphibian populations (Ouellet 2000).

RESULTS: GARTER SNAKES

This section summarizes the diet, distribution and movement patterns of garter snakes captured in Echo Basin from 2003 through 2006. Data presented here have also been included in a much broader analysis focusing on possible ecosystem-level indirect effects of fish stocking on regional native amphibians (see: Pope et al. *in review*).

Garter Snake Captures

A total of 351 garter snake observations were recorded from 2003 to 2006. During the mark-recapture component of the study (2004 to 2006), we marked a total of 95 common garter snakes and 58 aquatic garter snakes. Over the three years these marked individuals were captured a total of 229 times. We recaptured 24 individual common garter snakes from two to four times and 27 individual aquatic garter snakes from two to six times. Only 10 individual common garter snakes were recaptured between two years, and one between three years. Eleven individual aquatic garter snakes were recaptured between two years, and two between three years. Over the time sampled, the highest number of unique individuals found at a specific patch was 17 common garter snakes at SMP and 49 aquatic garter snakes at DPM (Figure 3).

Garter Snake Diets

We palpated 209 garter snakes in Upper Deep Creek basin from 2003 through 2006. Of the stomachs sampled, 38 (35.2%) of common garter snakes and 43 (42.6%) of aquatic garter snakes stomachs contained food items (Table 6). The diet of common garter snakes consisted entirely of amphibians with 90% of the stomachs sampled containing Cascades frogs. In contrast, aquatic garter snakes consumed both amphibians (44%) and brook trout (58%), with 89% of the amphibian prey being Cascades frogs. Both species of garter snakes consumed all age classes of amphibians, including large adult Cascades frogs, but most anuran prey consisted of larval or recent metamorphosed stages at traditional anuran breeding areas (Figure 9). One aquatic garter snake stomach contained a Cascades frog tadpole and a brook trout indicating individual snakes will move from fish bearing streams to amphibian breeding ponds to forage for both prey types. The number of prey items found in stomachs ranged from one to 16 for common garter snakes and one to 23 for aquatic garter snakes.

Garter Snake Spatial Patterns

Macrohabitat Use

Captures varied greatly between snake species based on hydrology. Common garter snakes were captured in lentic waterbodies 75% of the time, while 69% of the aquatic garter snake captures were captured in lotic areas (Figure 23). Few captures of either species were found upland in areas greater than 10 m from water.

Table 6. Diet composition of two species of garter snakes, 2003 through 2006, in Upper Deep Creek basin, Trinity Alps Wilderness, California.

		Common Garter Snake				*Aquatic Garter Snake*			
		Frequency		# of Prey		Frequency		# of Prey	
Prey Categories	Age Class[a]	*F* [b]	% *F* [c]	*N* [d]	% *N* [e]	*F* [b]	% *F* [c]	*N* [d]	% *N* [e]
		Native Prey							
Amphibian		38	100	158	100	19	44.2	69	72.6
Anura	L+J+A	36	94.7	156	98.7	19	44.2	69	72.6
Cascades frog	L+J+A	34	89.5	79	50.0	17	39.5	50	52.6
	L	16	42.1	41	25.9	13	30.2	46	48.4
	J	11	28.9	29	18.4	1	2.3	1	1.1
	A	9	23.7	9	5.7	3	7.0	3	3.2
Pacific Treefrog	L+J	9	23.7	77	48.7	4	9.3	19	20.0
	L	6	15.8	45	28.5	3	7.0	18	18.9
	J	3	7.9	32	20.3	1	2.3	1	1.1
Caudata	A	2	5.3	2	1.3	0	0	0	0
Long-toed Salamander	A	1	2.6	1	0.6	0	0	0	0
Unknown Salamander	A	1	2.6	1	0.6	0	0	0	0
		Non-native Prey							
Salmonidae	J+A	0	0	0	0	25	58.1	26	27.4
brook trout	J	0	0	0	0	11	25.6	11	11.6
brook trout	A	0	0	0	0	15	34.9	15	15.8
Total snakes sampled (N):		108				101			
Total stomachs containing prey (n):		38 (35.2%)				43 (42.6%)			

[a] Age class category of prey; Amphibian: L = Larvae (Tadpoles), J = Juvenile (< 50mm SUL), A = Adult (≥ 50mm SUL); Salmonidae: J = Juvenile (<100mm TL), A = Adult (≥100mm TL).

[b] Frequency of stomachs containing prey category. [c] Percent of stomachs containing prey category. [d] Total number of prey items for all stomachs combined. [e] Proportion of prey items for all stomachs combined. Some stomachs contained more than one prey category so percent values do not total to 100 for combined categories.

In addition to hydrologic differences, observations for each garter snake species differed based on their respective prey options (Figure 24). Observations of common garter snakes occurred most often at commonly used anuran breeding sites (80%) and less often (14%) in areas containing non-native brook trout. In contrast, aquatic garter snakes were observed most often in areas with non-native brook trout (92%). Aquatic garter snakes were also found in areas containing tadpoles 36% of the time, largely because one zone (DPMC) contained both non-native brook trout and multiple anuran breeding ponds.

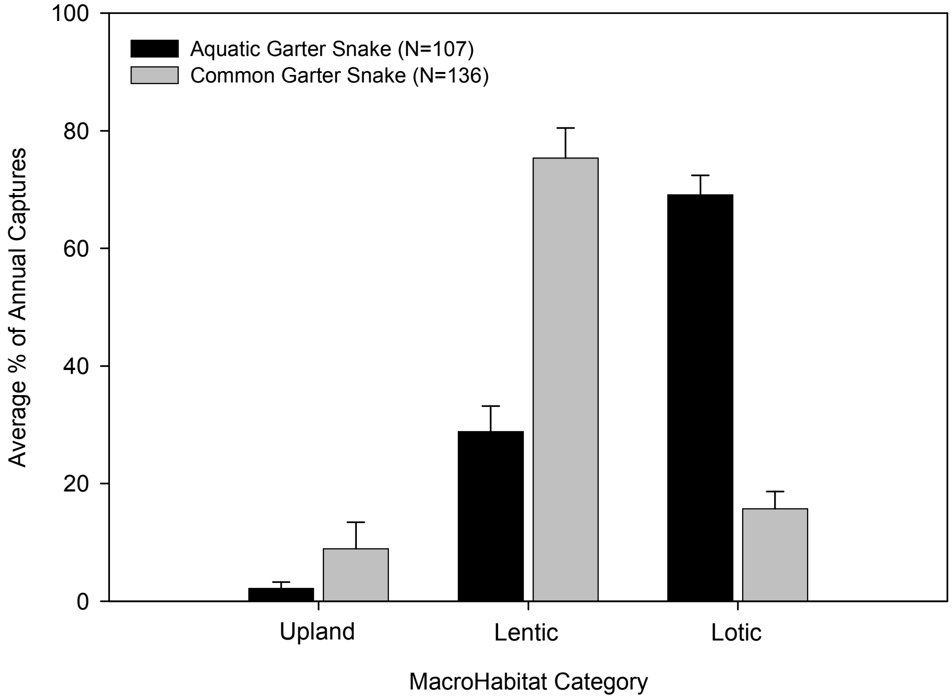


Figure 23. Mean Percent of captures, 2004 to 2006, for two species of garter snake by macrohabitat in upper Deep Creek basin, Trinity Alps Wilderness, California. Upland locations were greater than five meters from water; lentic locations included all captures in ponds and Echo Lake; lotic locations included all captures in streams. Error bars represent one standard error.

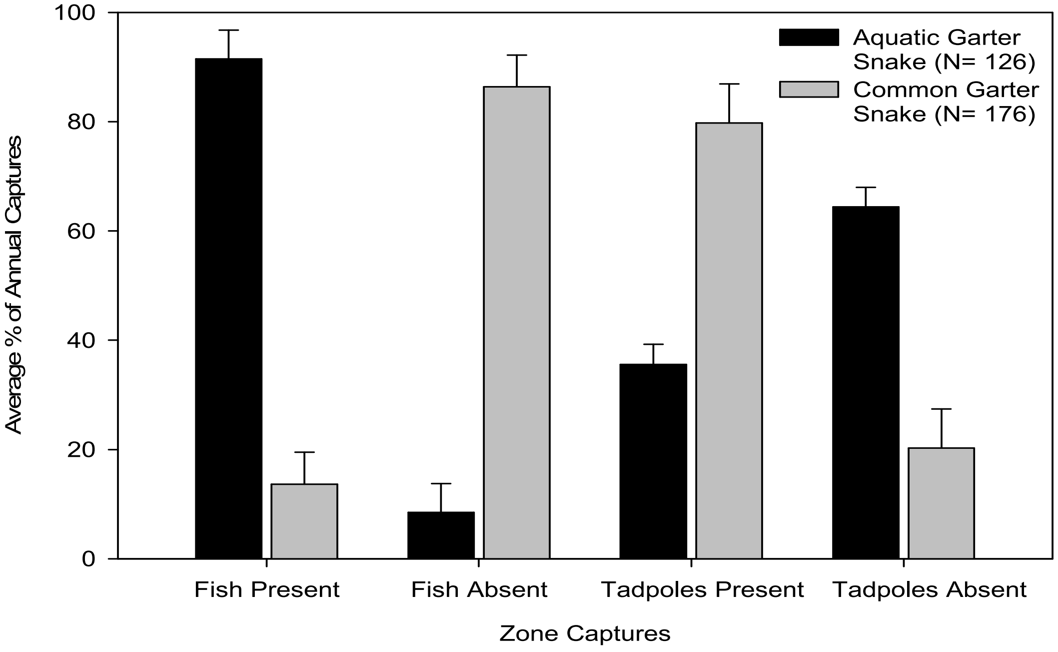


Figure 24. Mean Percent of annual garter snake captures (2003 to 2006) found in habitat zones with and without specific prey (fish or amphibian larvae), in upper Deep Creek basin, Trinity Alps Wilderness, California.

Movement

The longest movement observed by a common garter snake was 910 m, whereas the longest movement of an aquatic garter snake was 662 m. Both of these movements were round-trip migrations between two locations. On average, common garter snakes (*n* = 21) moved over twice as far (mean: 163 ± 37 m, range: 0 to 590m) as aquatic garter snakes (*n* = 27) (mean: 76 ± 23 m, range: 0 to 597 m). The net movement of common garter snakes was significantly greater than aquatic garter snakes (Mann-Whitney *U* test: $Z = 1.82$, $P = 0.034$). Of the common garter snakes captured more than one time, 48% (10) moved between habitat patches separated by 50 to 400 m. In contrast, only 11% (3) of aquatic garter snakes moved between habitat patches separated by 50 to 210 m.

RESULTS: TROUT, SNAKE, AND FROG DISTRIBUTIONS

Based on DFG stocking records, brook trout have been established in Echo Lake basin for a minimum of 78 years. Multiple gill nets were deployed in Echo Lake by Karen Pope (*USFS/ UC Davis*) from the fall of 2003 through the spring of 2005 as part of a trout removal experiment at four lakes in the Trinity Alps Wilderness. The brook trout population at Echo Lake was quickly depleted, and multiple subsequent net sets failed to capture fish. Only 56 fish were removed from Echo Lake and gill netting ceased in the spring of 2005 because extirpation was assumed complete. No fish were seen in the lake until the fall of 2006 when one brook trout fry was observed (K. Pope, unpubl. data, *USFS/ UC Davis*). Although fish were not successfully removed from Echo Lake, populations were greatly reduced from 2004 to 2006. We assume that gill nets failed to capture trout fry because the nets are size selective toward fishes > 80mm long. On 17 August 2007, J. Garwood counted 33 brook trout fry in Echo Lake where two spring streams enter into the lake. Interestingly, these fry appeared to be using the small spring inflows as thermal refugia; lake temperature away from these springs was 19.3ºC at 10:52. Based on these observations, it appears the Echo Lake fish population is expanding to pre-removal numbers through in-lake reproductive success.

By surveying the entire basin, we found brook trout have successfully invaded approximately 650 m of stream through Echo Lake's seasonal outlet. We also found brook trout present in Deep Creek gorge located below our study site, but physical barriers limited upstream movements of these trout. In addition to Echo Lake, brook trout were found in the low gradient portion of Deep Creek meadows (zones A to G) and adjoining Van Matre Creek fork (zones A to C) (Figure 3). The current fish distribution is likely constrained by a combination of high stream gradients, intermittent streams, and physical barriers within the remainder of the basin. Overall, spawning habitat in these streams was limited, but abundant gravels were present in DPMC and many brook trout were seen creating redds and spawning there annually during the month of September. Streams where trout did occur had robust numbers of individuals with well defined size class distributions. Our abundance estimate of brook trout in DPM totaled 395 fish with an average density exceeding two fish per meter of stream (Table 7).

Table 7. Estimated brook trout abundance in Deep Creek Meadows (DPM) calculated from bounded dive counts during the summer of 2005, Trinity Alps Wilderness, California.

Habitat Zone	Meters Searched[a]	Total Fish	# Fish/m of Stream[b]
DPMA	5.5	2	0.36
DPMB	73	300	4.11
DPMC	40.6	61	1.5
DPMD	19.4	7	0.36
DPME	30.2	18	0.6
DPMF	15.5	6	0.39
DPMG	1.6	1	0.63
Totals:	**185.8**	**395**	**2.13**

[a] *represents the sum of all habitat feature lengths that were searched for trout.*

[b] *Density of brook trout based on abundance estimates per linier meter of stream searched.*

Species Distributions and Densities

Kernel distributions of Cascades frogs and both garter snake species, as well as relative densities of brook trout, are displayed in Figure 25. Sixty three percent of the distribution kernel for aquatic garter snakes encompassed the trout-containing habitat compared to 11% of the distribution kernel for common garter snakes ($\chi^2 = 48.9$, $P < 0.0001$). Moreover, only 23% of the kernel for aquatic garter snakes overlapped with the kernel for Cascades frogs compared to 63% of the kernel for common garter snakes ($\chi^2 = 24.8$, $P < 0.0001$).

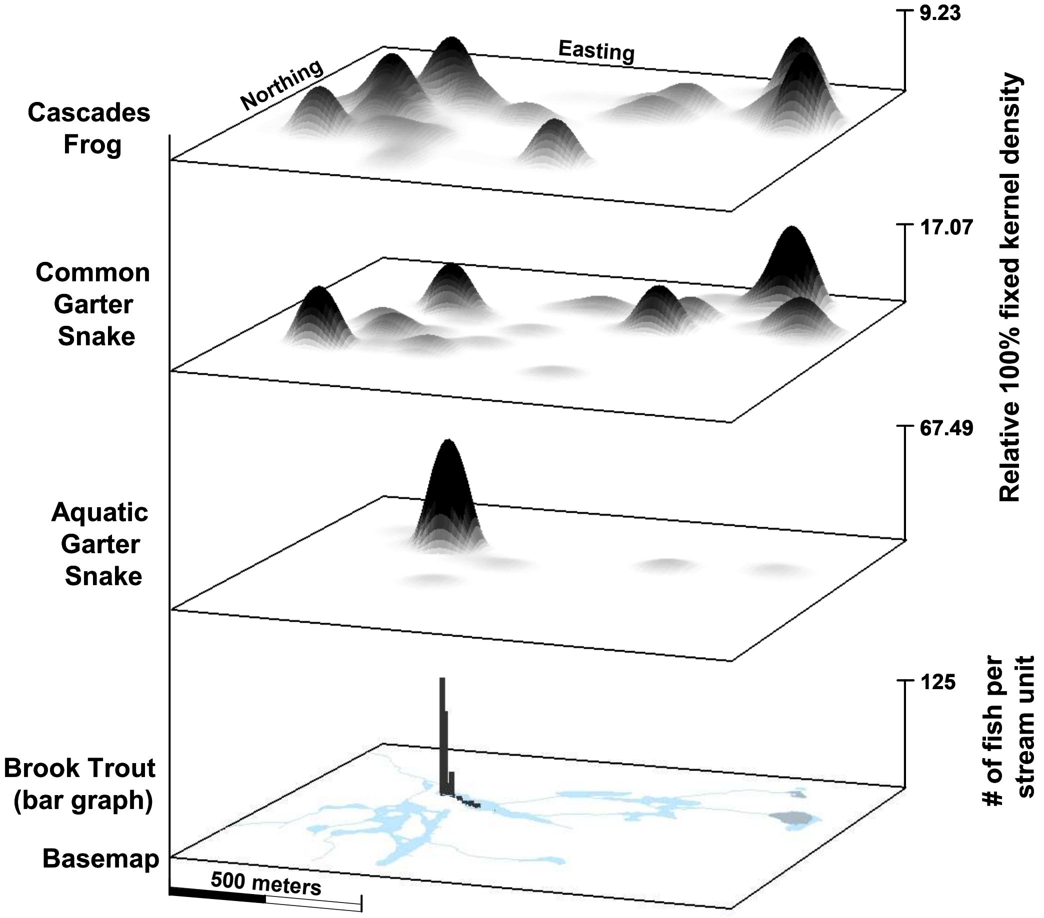


Figure 25. Fixed-kernel utilization distributions (bandwidth = 100) for Cascades frog, common garter snake, and aquatic garter snake locations within Deep Creek Basin, Trinity Alps Wilderness, California. The height of the density function depicts the relative probability of an individual occurring at each location within the study area. Relative kernel heights are estimated independently for each species and are not comparable across species. The bottom panel shows aquatic habitats within Deep Creek Basin and includes a spatially related bar graph representing estimated densities of brook trout in the basin.

Neighborhood Influences

We captured 456 uniquely marked Cascades frogs at three patches sympatric with non-native brook trout throughout Echo Lake basin from 2003 to 2007. Since Cascades frogs move often, we found 234 (51%) of these frogs were also captured in 14 other habitat patches reaching up to 1508 m away. The mean distance individual frogs traveled between patches with brook trout and surrounding fishless habitats was 421 ± 16.6 m (range: 70 to 1508 m).

Stream Densities of Cascades Frogs

During the summer foraging period, we found Cascades frog densities to be 6.3 times higher in LVM without brook trout (mean captures: 11.9 ± 1.2 frogs, max: 21) than in DPM with brook trout (mean captures:1.8 ± 0.3 frogs, max: 6) (Figure 26). These results are based on 21 independent surveys of these two streams from 2003 to 2006.

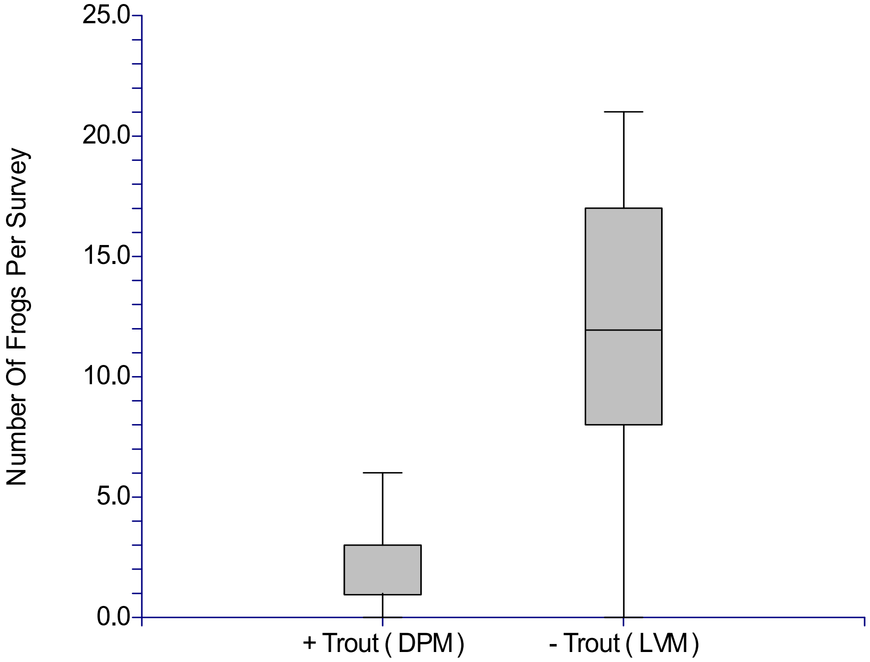


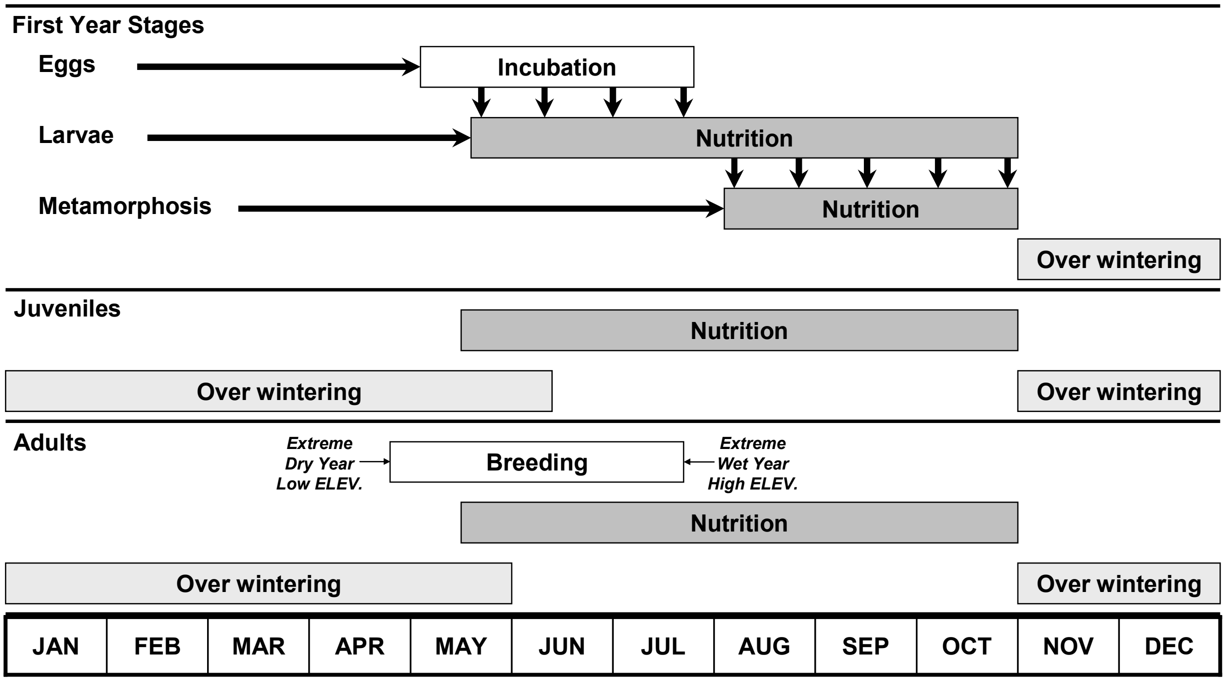
Figure 26. Box plots comparing Cascades frog captures at two stream reaches (190 m long), one with trout and one without trout in Echo Lake basin, Trinity Alps Wilderness, California. Both streams were located within 100 m, both had similar slopes, discharge and riparian vegetation characteristics.

DISCUSSION

Cascades frog Ecology

This study examined the timing and duration of specific annual life history attributes for Cascades frogs as well as ecological limits posed on this species in a high-elevation ecosystem (Figure 27). Overall, we found Cascades frogs to be quite resilient in this highly variable environment, by adjusting their behavior and habitat use as sites, seasons and years varied. It's important to note this study took place within a region (both Echo and Siligo basins) which we consider to have substantial amounts of exceptional habitats for Cascades frogs. Of the likely hundreds of basins these frogs inhabit across their range, it's important to consider that each basin or drainage has its own structural composition of aquatic resources, and thereby different pressures are exerted on species that inhabit them. However, based on a large elevational gradient and diverse assemblage of aquatic habitats, we suggest this study captured environmental variation that exists across much of the Cascades frog range in California.

Figure 27. Empirical model displaying timing and duration of specific life history attributes for all age classes of Cascades frogs from 2003 to 2007 in Echo Lake basin, Trinity Alps Wilderness, CA. Some life history attributes overlap due to geographic variation in snowmelt and or site availability/ elevations within the basin. Timing and duration of each life history attribute included data from 2006 (extremely wet year with 251% snowpack), and data from 2007(dry year with 38% snowpack) so extreme annual variability is represented.



Surveys and Captures

Based on annual captures, Cascades frogs were most active during the mid-summer months when temperatures were warm and between the hours of 1000 and 1700. This pattern is similar to what Pope (1999) discovered with Mountain Yellow-legged frogs, with the most captures occurring from August to mid-September in the High Sierra Nevada mountains. Outside of this period, we noticed captures were extremely variable based on age class and gender. For example, during the breeding season we primarily captured adult males concentrated around breeding ponds. Although active, we found gravid adult females to be quite cryptic during the spring which resulted in far fewer captures. Cryptic behavior of adult females during breeding seasons has been observed with other ranid frogs, with operational sex ratios of captures found to be extremely male bias (Davis and Verrell 2005, Wheeler 2007). In addition to adult females, we also captured few juvenile Cascades frogs during the spring. At this time most habitats were flooded with cold meltwater (sheet flow) and little to no vegetation was available in riparian areas during this time. Conditions during the early spring appear to be unfavorable for non-breeding cohorts based on limited foraging and basking opportunities, but this warrants more investigation.

In contrast to the spring, fall captures of Cascades frogs appeared to be bias toward YOPY and adult females. In addition we noticed that recent metamorphosed Cascades frogs were also active during this period. Because we saw more of the youngest age classes (smallest frogs) as well as adult females (largest frogs) during the late fall, we suspect this is the result of both having high energetic costs. For example, small frogs lack extra fat storage reserves for overwintering, whereas adult females were over twice as large as adult males, and must develop extra fat storage for egg development. We suggest these age/ sex groups must remain actively foraging late into the fall based on these suspected constraints. Future survey protocols and population level monitoring should account for this capture variation, especially when employing snapshot visual encounter survey techniques.

This study also determined annual reproductive output of Cascades frogs through egg mass counts. Since Cascades frogs are explosive breeders at specific sites, and breed in simple structured habitats with little vegetation, we found egg mass counts can be an efficient method and are near 100% accurate in determining total annual reproductive output, but see Garwood et al. (2007) for precautions on this method on Cascades frogs. These counts can be used as a tool for monitoring the effective size of breeding populations in a relatively short period. Our study was able to determine annual reproductive output over five years, with the length of breeding season averaging 58 days for the entire basin. We found, based on egg development rates, total annual egg production for this population could be obtained in four survey trips. Furthermore, egg mass counts can be especially useful in areas that have suffered significant declines, such as the Lassen region where egg masses were found more commonly than frogs in single surveys (Stead and Pope 2007, J. Garwood pers. obs.).

Habitats and Movements

Sinsch (1990) was the first to note that environments must provide a variety of resources for annual activities of anurans. These include wintering, aestivation, reproduction and foraging. These resources can be provided at a single location, however many of these seasonal resources are spatially separated for species in temperate areas. Recent studies of high-elevation temperate ranid frogs elucidate this point and show that individual frogs move between resources based on seasonal life history requirements including breeding, summer foraging and wintering habitats (Matthews and Pope 1999, Pilliod et al. 2002). Our information gathered on movement patterns and habitat use of Cascades frogs clearly demonstrates they use a variety of habitats that are spatially or temporally separated.

Ontogenetic shifts in habitat use was apparent in Echo Lake basin. We found that YOPY frogs were strongly associated with their natal breeding sites, and the majority were captured within 25 m of these areas. Based on snake densities at breeding sites, we believe YOPY frogs have a greater risk from predation than juvenile or adult frogs which were found in a greater variety of habitats. Specifically, juvenile frogs were found using summer-only ephemeral habitats more than twice as often as any other age class. In addition, juvenile frogs were also found to use streams more often than any other age class. Adult frogs had the highest variety of habitat use, but were found most often in perennial habitats. We believe adult frogs need the widest variety of habitats because they have more complex life histories that include reproduction.

Based on observations at both breeding and over-wintering locations groundwater springs were found to be highly important to Cascades frogs in this basin. During the breeding season, many groundwater spring ponds were the first to thaw, presumably due to water temperatures having little fluctuation where they surface. In total, 28 out of 38 breeding ponds (73%) were spring fed, with most having a year-round water supply. Springs were also important in the fall when aquatic resources were most limited in the basin and were the only water source remaining for many isolated places. We captured many frogs into October and again the following spring at the same spring pond locations. These spring sites do not freeze and have constant water temperatures throughout the winter months (J. Garwood, unpubl. data). Unlike Mountain-Yellow legged frogs which need deep lentic sites to over-winter (Bradford 1983), we found Cascades frogs over-wintering in spring fed areas that were sometimes less than 0.5 m deep. The most notable frog over-wintering site outside of springs in the basin was Echo Lake, but most frogs that over-wintered there were adult animals due to the low productivity at that site from 2003 to 2006.

We found Cascades frogs life history and population structure was strongly dependent on ecological processes operating at the basin level. Patches had such high connectivity from both dispersing and migrating individuals (Figures 13 and 18), we believe basins containing patchy habitats lack demographic independence and metapopulation structure. Furthermore, we found dispersal between basins was high, so at a minimum, the Cascades frogs in Echo Lake basin operate as a sub-population. Our results support the opinions of Smith and Green (2005) who, in their review on amphibian movements studies, found most studies covered areas too small to predict actual movement capabilities and population structure. Many studies resulted in falsely stating amphibians had low vagility, and thereby warranted less protections for corridors or surrounding habitats for population-level processes.

Juvenile Cascades frogs exhibited exceptionally high dispersal rates from natal sites to all available patches in Echo Lake basin (Figure 18). This high frequency of permanent movements resulted in juveniles having low patch fidelity. This is the first study we are aware of that documents inter-basin dispersal of anurans over mountain passes. By surveying multiple basins, we found dispersal between them to not be a rare event, with 17 individuals moving between four basins within five years. Based on our minimal survey effort in these proximal basins, we suggest this is a low estimate of these movements. For example, the only proximal site surveyed regularly was Red Mountain meadows where we found six out of 15 (40%) individual frogs that were originally captured and marked in Echo Lake basin. These movements demonstrate inter-basin connectivity can be high, even when the landscape lacks aquatic features for greater than 500 m. Furthermore, these results are evidence that gene flow among adjacent basins are within the accepted levels for maintaining genetic diversity between sub-populations (Mills and Allendorf 1996) by having greater than one individual per generation dispersing over mountain passes. The connectivity of frog populations among basins should be taken into consideration when managing for this species.

Breeding Ecology

Each year, timing of breeding was largely dependent on winter snow accumulation and the elevation of each breeding site (Figure 22). This variation indicates Cascades frogs are explosive breeders at specific sites, but have extended breeding seasons annually. Based on our egg mass counts, Cascades frogs appear to have a relatively small effective population size in Echo Lake basin. Although 18 to 27 individual ponds and one lake were used for breeding annually, only a maximum of 47 to 80 egg masses were produced annually over the five years. For comparison, Briggs (1987) found from 21 to 43 egg masses annually in one pond that was only 550 m^2 at 1285 m in elevation.

Garter Snake Ecology

This study reveals that the two garter snake species appear to have different life history strategies. These differences may explain why these closely related species can co-exist in a relatively small and simplified food web. Specifically, we found the diet, distribution, movement and density differed greatly between the two species. The most striking observation was the utilization distributions of common garter snakes and aquatic garter snakes in Echo Lake basin (Figure 25). These distributions mirrored the distribution of their respective primary prey. Common garter snakes were strict amphibian predators whereas aquatic garter snakes consumed both amphibians and trout in near equal proportions. The majority of amphibians found in the basin were lentic breeders (Cascades and Treefrogs), and may explain why common garter snakes were found predominantly in lentic habitats, especially around amphibian breeding sites containing larvae. In contrast, aquatic garter snakes were found almost exclusively in and around streams containing brook trout. Since many Cascades frog breeding locations were near sites with fish, and predation by aquatic garter snakes was highest on frogs here in general, we suspect frogs are experiencing predation levels above what would be expected naturally. Possible landscape level consequences from our data have been incorporated into a much larger analysis that addresses this phenomenon across the Trinity Alps Wilderness (Pope et al. *in review*). At minimum, our results indicate that predators are influencing Cascades frog populations and introduced fishes have the potential to alter garter snake roles in food web dynamics.

Introduced Brook Trout

A large body of literature has implicated introduced fishes as a major source of amphibian declines in lakes of the Western United States (see Pilliod and Peterson (2001), and Kats and Ferrer 2003 for a review) most notably through direct predation on tadpoles and young frogs (Simons 1988, Vredenburg 2004). Welsh et al. (2006) found strong negative correlations with local amphibians at lakes with fish present, even when proximal fishless sites were accounted for in the analysis. Research currently being conducted in the Trinity Alps Wilderness (by Karen Pope *USFS/ UC Davis*) is addressing introduced trout effects on lentic waterbodies, and is using the Cascades frog as a focal species.

Introduced fish may pose a greater threat to successful recruitment of Cascades frogs at high elevation sites than at lower elevation sites. High elevation sites, such as Echo Lake, usually have very simple shorelines, primarily due to the lack of large wood and aquatic vegetation existing at lower elevation sites (H. Welsh unpubl. data). Since introduced trout are visual predators on amphibians (Vredenburg 2004), tadpoles and young frogs have less cover to protect themselves from predation by introduced fish. In addition, we only found 18 individual YOPY Cascades frogs at Echo Lake over 44 surveys from 2003 to the spring of 2007. During these years, when snowpack was above normal, we consistently saw tadpoles at Echo Lake in the late fall that failed to reach metamorphosis or over-winter. In contrast, in the fall of 2007 we found many metamorphosed individuals at the lake indicating drought years allow sufficient time for most tadpoles to metamorphose at this lake. Since Echo Lake only has the potential for effective recruitment in drought years (in this case one out of five years), introduced trout could pose a much larger threat to this already intermittent recruitment success through direct predation in drought years.

Breeding habitats proximal to lakes containing introduced fish have been found to buffer potential loss of frog recruitment, especially if effective reproduction occurs annually at these sites (Knapp et al. 2007). In Echo Lake basin and possibly others, we suggest this assumption could be falsely considered. We found most adults chose to migrate from the lake and use SMP, a nearby site, for reproduction. Each year, SMP dried completely by the fall though hundreds to thousands of tadpoles survived to metamorphosis. However, we only captured 30 YOPY that survived over-wintering at this site over the length of the study. All of these individuals were captured in the early spring and were found to be extremely emaciated; with only three of the 30 marked individuals recaptured. Furthermore, we failed to detect any overland migrations of these individuals, and patches closest to SMP never received an influx of metamorphosed frogs in the fall. So, even though a nearby site was available for reproduction, away from non-native trout, reproduction largely failed.

Although a large body of literature describes fish stocking effects on lakes throughout the Western U.S., few studies have looked into possible effects of introduced fish on native amphibians in basins that have streams associated with these lakes (Adams et al. 2001), but see Gillespie and Robertson (2001) and Bosch et al. (2006) for introduced fish effects on amphibians in other stream systems. Since DFG has focused its stocking and management efforts on lakes, little information exists on the invasion of these fishes into non-target and unmanaged areas, specifically streams associated with lakes containing introduced fish populations. Based on established protocols that are “lake” and “pond” focused, inventories of introduced fish and amphibian populations, at whole-basin scales, have possibly been grossly underestimated. For example, we found a robust brook trout population occupying 650 m of stream in Echo Lake basin. This population was greater than 750 m from the lake, though it was seeded directly through the outlet stream of the lake. Since our study showed Cascades frogs used streams most often during summer foraging, these habitats may have been largely overlooked for their importance in other studies. Furthermore, we found summer Cascades frog densities to be 6.3 times higher in a stream lacking trout than at a similar stream with high densities of brook trout. This suggests these unmanaged fish populations are negatively impacting Cascade frogs, but is in need of further study. Potential impacts posed by fish populations in streams could also affect other amphibian species. In addition to Cascades frogs, we found a population of tailed frogs (*Ascaphus truei*), another California Species of Special Concern (Jennings and Hayes 1994), distributed in five streams throughout the basin (Appendix D). We failed to find any tadpoles or frogs of this species in streams of similar discharge containing brook trout.

Finally, Cascades frogs found in patches with trout can be negatively impacted in a variety of ways. For example these effects can range from direct predation on frogs (Simons 1998), competition for food (Finlay and Vredenburg 2007), and indirectly through a shared predator (Zavaleta et al. 2001, Pope et al. *in review*). Since Cascades frogs demonstrated substantial dispersal and migration capabilities between separate patches, we suggest individual patches containing brook trout could have far reaching consequences beyond their limited distribution. Since the average distance a frog moved between a patch with and without brook trout was greater than 400 m, unknown population level consequences could result at patches well away from these fish. An example of such a population level consequence could be increased predation by aquatic garter snakes on adult frogs that would otherwise reproduce in a patch not containing fish. Though our study took place in only one basin, our look into possible impacts posed on Cascades frogs by introduced brook trout presents a compelling case study.

MANAGEMENT RECOMMENDATIONS

Within the last decade, DFG has initiated a conservation strategy for maintaining aquatic biodiversity in high-elevation wilderness ecosystems. This management objective aims to protect and enhance native amphibian species while attempting to optimize recreational trout fishing opportunities. Starting in 1999, DFG has been implementing this conservation strategy in the Sierra Nevada Mountains through watershed-based management plans (http://www.dfg.ca.gov/habcon/conproj/big_pine.html, C. Milliron, 2005). These plans are focused on basin-wide management of both native mountain (and Sierra) yellow-legged frogs (MLYF) and introduced fishes. We suggest these plans can also be successful for better managing aquatic species biodiversity across the range of Cascades frogs and other amphibian species in northern California.

However, ecosystem differences do exist between the Sierra Nevada Mountains and the regions where Cascades frogs are found. These differences provide a different set of design challenges for creating successful management plans. Although the Cascades frog is closely related to the MLYF, each species has specific and different ecological requirements. For example, Cascades frogs can breed in a wider variety of habitats than the MLYF because Cascades frogs do not require over wintering habitats for tadpoles. Additionally, the Klamath region holds the highest diversity of sub-alpine amphibian species in the western United States, with three species listed as California species of special concern. We encourage managers to use the results of this study as a tool for decision making that will benefit not only Cascades frogs and other native species, but recreational fisheries as well. Further, Cascades frog populations found in the Lassen and Shasta regions of California may also have different ecological dynamics than the population studied here in the Klamath Mountains. These populations need further study to reflect these potential regional differences. However, across their range in California, Cascades frogs have the same general annual life history patterns and exist in high-elevation snow driven systems. Our observations provide important insights based on a detailed long-term study. The following recommendations could be considered when designing management plans in areas with Cascades frogs present.

- Management decisions for Cascades frogs need to be addressed at scales relevant to whole populations. This study demonstrated Cascades frog populations can operate over a large area, with individuals moving between multiple habitat types for specific seasonal resources. We suggest that areas containing continuous Cascades frog habitats, or habitats isolated by one kilometer or more should be considered appropriate for assessing habitat quality, population demographics, and potential negative effects from fisheries management. Based on our study, we found the CalWaters watershed scale was possibly too large of an area to make informed management decisions on this species. For example, we found two distinct populations of Cascades frogs operating within the Deep creek drainage- a defined CalWaters drainage. These populations occurred in two distinct sub-basins within Deep creek drainage (Figure 2).

- When establishing basin inventories of Cascades frog populations, we suggest surveys should be conducted when conditions are most favorable for detecting all potential age classes. This study found the most favorable conditions for detecting all potential age classes during the mid-summer months. Detecting all age classes will allow managers to identify the minimum number of generations present in a given population, including the population's structure. Missing age cohorts could be a direct sign of habitat bottlenecks, weather induced impacts, a stressed population or disease. Obtaining length measurements from individual animals will help managers determine a population's structure before making informed management or restoration decisions. In addition, we found egg mass surveys are a rapid and easy tool for monitoring effective population sizes of Cascades frogs during breeding seasons. Determining breeding locations and effective population sizes allows managers to address and better understand both spatial attributes and reproductive output of populations.

- We suggest inventories of basins should incorporate more rigorous protocols for detecting natural amphibian predators, most specifically snakes (*Thamnophis spp.*). Based on our snake diet and distribution results, we suggest that finding common garter snakes in a basin could reflect a healthy amphibian community. Alternatively, finding many aquatic garter snakes in areas with fish could indicate altered food web dynamics and increased predation pressure on amphibians (see Pope et al. *in review*). Accounting for predators will give managers better insight on local food web dynamics and possible stressors to frog population dynamics.
- In addition to detecting amphibian predators, basin inventories could also include other sensitive amphibians (California species of special concern) that are palatable to fish, especially the tailed frog (*Ascaphus truei*) and long-toed salamanders (*Ambystoma macrodactylum*). This will require adding additional survey methods (i.e. night surveys of lentic and lotic habitats) more suited to detecting species with life histories that differ from Cascades frogs.
- Based on our findings, managers should consider all surface water in basins where Cascades frogs are found as potential habitat, this includes spring sources which we found to be important for both reproduction and wintering habitats. Since introduced fishes have commonly invaded aquatic resources outside of directly managed waterbodies (especially streams), managers should determine the full extent of fish distribution in basins before making informed management decisions. Additionally, habitats surrounding those with introduced fish should be identified based on a hydrological gradient (seasonal to perennial) and assessed as potential habitat for specific life history components (e.g. breeding, summer, and winter habitats) before making informed decisions on fisheries management.
- Where feasible, isolated habitat patches with both Cascades frogs and introduced fishes should receive increased protection through complete eradication of fish populations. Specifically, we suggest basins containing one to few lentic waterbodies separated by one kilometer or more from the nearest perennial Cascades frog breeding habitat should receive this type of restoration and increased protection.
- Maintaining gene flow between animal populations should be an important consideration for managers. This study showed that Cascades frogs use mountain passes as dispersal corridors, so we recommend that aquatic habitats closest in linking adjacent basins should have increased protection and should be a high restoration priority for maintaining gene flow among Cascades frog populations.

- High-elevation waterbodies (with Cascades frogs present or nearby) greater than 2,100 meters in elevation should also receive increased protection through complete eradication of introduced trout where feasible. This study showed that a high elevation breeding site may not produce successful Cascades frog offspring in heavy snow years, but were shown to have successful breeding recruitment of Cascades frogs during a drought year. Since Cascades frogs are long lived (>7 years), habitats with intermittent reproductive success can still provide important reproductive potential in favorable weather years. In addition, these high-elevation sites usually have reduced structural shoreline complexities from the lack of riparian vegetation. This lack of complexity may pose as greater predation risk by visual trout predators on tadpoles during key reproduction years.
- A selective fish eradication in the range of Cascades frogs could further the conservation of this frog species by buffering losses from potential outbreaks of infectious diseases. One such disease is chytridiomycosis caused by *Batrachochytrium dendrobatidis* (BD). BD has recently been detected in some Cascades frog populations within the Trinity Alps Wilderness (K. Pope pers. comm.) and should be of great concern to managers. This disease in particular has been noted to swiftly decrease or exterminate previously robust populations of amphibians worldwide and will remain a major challenge in managing local native amphibians. In the Sierra Nevada, both introduced trout and BD have been identified as major causes to extirpating historically robust populations of MLYF (Rachowicz et al. 2006).

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APPENDICES

Appendix A. Inclusive dates by census for Cascades frog visual encounter mark-recapture surveys including the number of newly marked animals totaled by census from years 2003 to 2007 in upper Deep Creek Basin, Trinity Alps Wilderness, California. Census durations varied, with spring and fall having the shortest time intervals.

Census	Start Date	End Date	# Newly Marked *R. cascadae*	# of Recaptured *R. cascadae*
1	4-Jun-2003	5-Jun-2003	26	0
2	10-Jun-2003	15-Jun-2003	185	3
3	19-Jun-2003	26-Jun-2003	161	48
4	30-Jun-2003	10-Jul-2003	193	98
5	15-Jul-2003	25-Jul-2003	148	137
6	28-Jul-2003	8-Aug-2003	108	173
7	11-Aug-2003	20-Aug-2003	67	177
8	20-Aug-2003	15-Sep-2003	32	161
9	18-Sep-2003	22-Sep-2003	16	64
10	2-Oct-2003	23-Oct-2003	10	79
11	25-May-2004	26-May-2004	4	20
12	5-Jun-2004	8-Jun-2004	12	44
13	17-Jun-2004	22-Jun-2004	60	120
14	25-Jun-2004	5-Jul-2004	67	211
15	9-Jul-2004	17-Jul-2004	60	215
16	22-Jul-2004	28-Jul-2004	28	187
17	2-Aug-2004	8-Aug-2004	41	188
18	8-Aug-2004	20-Aug-2004	16	159
19	25-Aug-2004	5-Sep-2004	15	179
20	8-Sep-2004	26-Sep-2004	5	140
21	1-Oct-2004	10-Oct-2004	5	93
22	30-May-2005	31-May-2005	1	24
23	11-Jun-2005	14-Jun-2005	4	40
24	22-Jun-2005	24-Jun-2005	10	60
25	29-Jun-2005	3-Jul-2005	41	121
26	4-Jul-2005	21-Jul-2005	161	178
27	27-Jul-2005	2-Aug-2005	72	165
28	9-Aug-2005	16-Aug-2005	36	216
29	22-Aug-2005	1-Sep-2005	25	171
30	6-Sep-2005	14-Sep-2005	17	183
31	20-Sep-2005	25-Sep-2005	36	119
32	10-Oct-2005	12-Oct-2005	4	80
33	31-May-2006	31-May-2006	0	21
34	14-Jun-2006	28-Jun-2006	0	27
35	10-Jul-2006	13-Jul-2006	0	83
36	17-Jul-2006	29-Jul-2006	4	130
37	9-Aug-2006	23-Aug-2006	4	132
38	6-Sep-2006	10-Sep-2006	8	136
39	6-Oct-2006	10-Oct-2006	0	37
40	28-Apr-2007	29-Apr-2007	8	32
41	8-May-2007	20-May-2007	1	19
42	27-May-2007	9-Jun-2007	24	133
43	17-Jun-2007	22-Jun-2007	23	38
44	2-Jul-2007	8-Jul-2007	20	63

Appendix B. Summary of all Cascades frog captures by year, site, and census period from 2003 to 2007 in Echo Lake basin, Trinity Alps Wilderness, California. Dashes indicate a site was not surveyed during a specific census.

	2003											2004											2005											2006							2007					
Census:	1	2	3	4	5	6	7	8	9	10		11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	
Site	**Echo Lake Basin**																																													Totals
BLB	0	0	2	1	0	0	0	1	0	0		0	0	5	2	3	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	–	–	–	1	–	18
CAS	0	16	38	37	14	14	12	7	0	5		3	8	9	9	3	3	4	5	8	3	4	1	1	5	5	4	1	5	7	11	4	6	0	3	5	0	4	5	5	6	8	0	2	2	292
CLM	0	0	0	12	16	12	6	5	0	0		0	0	5	17	10	4	12	6	5	5	0	0	0	1	8	9	5	7	1	0	0	1	0	0	7	6	7	2	0	0	1	5	–	–	175
DPM	15	55	100	91	48	28	33	23	1	8		21	37	37	27	20	21	21	18	24	23	20	21	26	24	23	15	16	11	14	23	4	22	21	7	6	5	8	14	12	34	2	10	8	4	1001
ECH	11	19	22	10	34	119	56	62	38	50		0	0	9	19	59	47	41	48	41	36	23	0	3	3	12	36	33	43	32	28	8	10	0	1	7	46	46	36	7	0	0	45	9	10	1159
EVM	0	1	1	22	28	28	17	8	1	0		0	0	7	29	28	22	34	19	32	14	6	0	0	1	5	14	12	20	16	10	11	4	0	0	5	4	4	7	0	0	–	4	–	2	416
GSP	0	1	0	17	10	19	22	19	6	4		0	3	13	10	13	10	8	9	7	1	4	0	0	0	10	11	6	9	4	4	2	0	0	2	6	0	4	2	4	0	0	1	–	1	242
LVM	0	1	3	28	22	16	9	16	8	5		0	1	9	20	19	23	20	7	17	20	11	0	0	6	8	13	20	21	16	12	13	9	0	2	10	10	14	12	2	0	0	4	2	11	440
MOS	0	4	18	5	6	2	3	1	0	3		0	0	24	13	14	4	13	7	12	2	0	0	5	6	12	4	4	9	1	9	9	4	0	2	0	1	2	1	2	0	–	1	–	–	203
MVM	0	0	17	14	17	6	11	8	0	5		0	1	19	37	34	25	12	17	17	15	9	0	7	10	12	35	25	21	17	29	17	5	0	3	1	4	7	14	1	0	–	3	–	–	475
PTH	0	0	0	2	11	15	8	8	10	6		0	3	13	6	7	11	10	8	4	2	4	2	2	4	5	15	33	39	23	23	27	6	0	0	5	4	0	17	1	0	0	13	12	13	372
UVM	0	0	3	5	15	8	18	17	8	1		0	0	8	17	10	12	14	5	12	7	10	0	0	5	16	26	29	15	23	21	12	10	0	0	9	9	7	7	4	0	4	5	–	–	372
SMP	0	0	4	25	46	29	8	15	6	7		0	0	4	57	20	17	16	7	6	7	3	1	0	3	8	25	32	29	15	17	7	5	0	7	19	38	29	18	0	0	0	34	–	2	566
VMC	–	–	–	18	9	6	6	1	0	0		0	0	1	9	11	8	4	6	2	4	2	0	0	0	3	8	7	5	4	5	3	2	0	0	0	4	4	3	0	0	–	–	–	–	135
EDN	–	–	–	–	–	–	–	–	–	–		–	–	–	–	11	4	7	10	6	4	2	0	0	1	8	22	13	6	7	6	0	0	0	0	2	3	0	6	0	0	–	5	–	–	123
DPC	–	–	–	–	1	–	–	–	–	–		–	–	–	1	1	–	9	3	1	–	–	–	–	1	–	5	–	4	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	27
VAG	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	3
BBL	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–	0
ELV*	–	–	–	3	1	10	5	1	–	–		–	–	–	1	5	2	1	–	–	–	–	–	–	–	–	2	1	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	35
Echo Lake Basin Total:																																														**6054**
	Peripheral Sites Outside Of Echo Lake Basin																																													
RMM	0	0	1	1	1	2	2	1	2	1		0	3	4	4	0	2	0	0	0	1	0	0	0	0	2	0	0	1	1	2	0	0	–	–	–	–	–	–	–	–	5	–	–	–	35
BBD	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	3	–	–	–	–	–	–	–	1	–	–	–	–	–	2	7
ATL	–	–	–	–	–	–	–	–	–	–		–	–	13	–	7	–	–	–	–	–	–	–	–	–	24	–	–	–	–	–	27	–	–	–	–	–	–	–	–	–	–	–	–	–	71
FOX	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2
TAL	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8
BOB	–	–	–	–	–	–	–	–	–	–		–	–	–	39	–	–	–	–	–	–	–	–	–	–	–	76	–	–	5	–	–	–	–	–	–	–	–	–	–	–	–	6	8	10	144
DAR	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	22	–	–	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	28
DEE	–	–	–	–	1	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
USL	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	26	–	–	20	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	46
USC	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	16	–	3	17	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	36
MSM	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	42	–	–	–	–	10	–	–	–	–	–	–	–	–	–	–	12	11	17	92
SIC	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
GDP	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	20	–	1	7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	28
SSL	–	–	–	–	–	–	–	–	–	–		–	–	–	30	–	–	–	–	–	–	–	–	–	–	–	75	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7	6	4	122
LSI	–	91	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2	4	8
Peripheral Site Total:																																														**631**
Totals:	26	188	209	291	280	314	216	193	80	95	0	24	56	180	347	275	215	229	175	194	145	98	25	44	70	162	521	237	252	248	204	155	84	21	27	83	134	136	145	38	40	20	157	61	83	**6685**

**Indicates incidental captures outside of established habitat patches.*

Appendix C. Summary table of attributes, movement, and fate of 51Cascades frogs monitored by radio telemetry for years 2003 and 2004 in Echo Lake basin, Trinity Alps Wilderness, California.

ID.	Sex	SUL	Weight (g)	Radio Weight % (g)	Dates Monitored	Tracking Duration (Days)	Fixes	Dist Sum (m)[a]	Maximum Displacement (m)[b]	Fate
1	F	56.2	16.8	5.0	13 Aug-1 Sep 03	19	12	210	141	Radio battery expired, could not locate
2	F	73.7	42.4	2.4	17 Aug-3 Oct 03	47	13	252	179	Radio battery expired, could not locate
3	M	57.0	19.7	5.2	6 Jul-1 Sep 03	57	33	518	306	Suspect *Thamnophis* spp. predation
4	M	57.7	18.7	4.5	21 Jun-22 Sep 03	93	45	263	117	Radio battery expired, could not locate
5	M	59.3	21.5	4.7	24 Jun-22 Aug 03	59	35	1171	260	Released, abrasion on stomach
6	F	65.3	32.5	3.1	21 Jun-12 Aug 03	52	25	747	592	Released, abrasion on hip and stomach
7	F	53.5	15.9	5.3	20 Jun-12 Aug 03	53	31	204	70	Released, abrasion on urostyle and stomach
8	M	57.6	19.5	4.4	24 Jun-5 Aug 03	42	30	829	408	Released, abrasion on stomach
9	M	56.5	21.7	3.9	20 Jun-12 Sep 03	84	37	1342	255	Radio battery expired, could not locate
10	F	61.2	24.5	4.2	23 Aug-15 Sep 03	23	9	409	337	Predation: *Thamnophis sirtalis*-Length: 70cm
11	F	60.0	27.7	3.7	23 Jun-4 Aug 03	42	26	348	261	Released, abrasion on dorso-lateral folds
12	M	57.7	22.5	4.5	21 Jun-23 Jun 03	2	3	57	49	Predation: *Thamnophis atratus*- Length: 85cm
13	M	58.8	20.9	4.1	20 Jun-24 Aug 03	65	40	1132	373	Radio battery expired, could not locate
14	F	68.5	28.8	3.5	18 Jul-15 Sep 03	59	32	839	424	Released
15	F	70.9	30.7	3.3	18 Jul-5 Aug 03	18	14	316	88	Predation: *Thamnophis sirtalis*- Length: 72cm
16	M	58.2	17.9	5.7	13 Aug-2 Oct 03	50	20	247	80	Released
17	F	59.7	22.3	4.6	24 Jun-17 Jul 03	23	13	221	161	Released, abrasion on dorso-lateral folds
18	M	60.0	17	6.0	13 Aug-2 Oct 03	50	21	368	57	Released, abrasion on dorso-lateral folds
19	F	64.1	28.6	3.6	8 Jul-4 Aug 03	27	16	263	66	Released, abrasion on side and stomach
20	F	63.0	27.5	3.7	5 Jul-17 Jul 03	12	7	185	102	Radio battery expired, could not locate
21	M	58.9	20.9	3.9	18 Jun-3 Jul 04	15	8	19	11	Shed radio
22	M	60.1	21.3	3.8	19 Jun-29 Jun 04	10	7	347	253	Released
23	F	63.6	23	4.6	19 Jun-20 Jun 04	2	2	218	218	Shed radio
24	F	75.5	39.1	2.7	20 Jun-26 Jun 04	6	3	3	3	Shed radio
25	F	71.3	35.4	3.0	20 Jun 04	1	1	—	—	Shed radio
26	F	73.2	31	3.4	20 Jun-26 Jun 04	6	3	11	10	Shed radio
27	M	58.9	18.5	5.7	21 Jun-13 Jul 04	22	10	141	120	Radio battery expired, could not locate
28	M	63.9	21.9	4.8	21 Jun-2 Jul 04	11	6	73	36	Shed radio
29	F	74.7	36.6	2.9	21 Jun-3 Oct 04	104	38	416	271	Released
30	M	59.8	20.4	5.1	21 Jun-10 Oct 04	111	42	357	67	Shed radio, found later and tracked again.

Appendix C. Continued.

ID.	Sex	SUL	Weight (g)	Radio Weight % (g)	Dates Monitored	Tracking Duration (Days)	Fixes	Dist Sum (m)[a]	Maximum Displacement (m)[b]	Fate
31	M	60.0	20.1	5.2	21 Jun-3 Aug 04	43	18	91	34	Released, abrasion on right side
32	F	62.7	20.9	5.0	26 Jun-28 Jul 04	32	16	217	162	Predation: *Thamnophis sirtalis*
33	F	77.9	35.5	3.0	27 Jun-10 Oct 04	105	43	830	191	Released
34	F	67.0	22.5	4.7	27 Jun-9 Oct 04	104	44	408	112	Released
33	F	77.9	35.5	3.0	27 Jun-10 Oct 04	105	43	830	191	Released
34	F	67.0	22.5	4.7	27 Jun-9 Oct 04	104	44	408	112	Released
35	F	66.9	27.9	3.6	29 Jun-10 Oct 04	103	39	259	59	Released
36	M	55.8	13.8	5.8	2 Jul-8 Oct 04	98	37	1009	326	Released
37	F	63.0	20.7	5.1	10 Jul-17 Jul 04	7	6	49	26	Predation: *Thamnophis atratus*
38	F	67.8	17.9	5.9	12 Jul-8 Aug 04	27	16	301	77	Predation: *Thamnophis sirtalis*
39	M	56.2	17	6.2	12 Jul-17 Jul 04	5	5	18	10	Shed radio
40	F	62.7	19	5.5	13 Jul-27 Aug 04	45	22	138	63	Predation: *Thamnophis sirtalis*- Length: 73cm
41	F	56.8	16.3	4.7	23 Jul-10 Oct 04	79	31	211	100	Released
42	M	61.1	19.8	5.3	23 Jul-10 Oct 04	79	30	272	136	Released
43	F	70.0	25.9	4.1	23 Jul-8 Aug 04	16	8	15	4	Mortality of unknown cause, desiccated
44	F	76.5	39.8	2.7	26 Jul-3 Oct 04	69	27	264	132	Shed radio
45	M	59.3	18.5	5.4	28 Jul-3 Aug 04	7	2	10	10	Radio battery expired, could not locate
46	F	67.4	24.4	4.1	6 Aug-4 Sep 04	30	2	14	14	Released, abrasion on dorso-lateral folds
47	M	58.8	16.6	6.3	18 Aug-4 Sep 04	17	6	15	5	Released
48	F	73.6	31.5	3.2	20 Aug-8 Oct 04	49	15	50	14	Released
49	F	73.8	37.9	2.6	4 Sep-10 Oct 04	36	13	140	71	Released
50	F	63.9	22.5	3.6	9 Sep-10 Oct 04	31	10	174	112	Released
51	M	56.6	17	6.2	19 Jun 04	1	1	—	—	Shed radio

[a] *Cumulative distance traveled by an individual over its entire tracking period.*
[b] *Distance separating the furthest two telemetry locations for each individual representing the maximum displacement.*

Appendix D. Non-target herpetofauna detected during this study in the southeast Trinity Alps Wilderness from 2003 to 2007.

Species	Occurrence	Years Noted	Occurrence Notes	Life Stages Observed
Amphibia				
Caudata				
Long-toed Salamander ***Ambystoma macrodactylum***	Regionally rare Common at one locality	5	Rare in Siligo and Echo Lake basin. Observed 22 and 21 larvae at SMP in 2003 and 2004 respectively. Also observed one larva at Bob's meadow. This species have a two year larval stage at these high elevations and larvae cannot survive to metamorphosis at this pond because it dries completely each fall. Observed one larva in 2006 at Echo lake; we assume brook trout to be a major predator here because larvae are commonly found in exposed open-water areas in Billy-Be-Damned lake which is fishless. Larvae were common annually from 2005 to 2007 when we surveyed Billy-Be-Damned Lake; we noticed two distinct larval age classes at this site. Adults rarely seen and are only on the surface during their explosive breeding season (< 1 week) at first thaw. Observed one adult at SMP in 2006.	Larvae Adult
Rough-skinned Newt ***Taricha granulosa***	Regionally rare	3	Observed one large adult female on six occasions in the same pond at DPM for years 2003, 2004 and 2007. We assume this is a single animal. Seen nowhere else where we conducted surveys.	Adult
Ensatina ***Ensatina eschscholtzii***	Rarely detected	1	Found one adult on Stuarts Fork trail (Bridge Camp) ~ 1 km below the mouth of Deep creek on 07 Oct 2007. Found one possible juvenile individual (31mm SVL) in the stomach of a *T. sirtalis* at Echo lake in 2004: genetic analysis pending. Our survey protocol was not designed to detect this terrestrial species.	Juvenile? Adult
Anura				
Coastal Tailed Frog ***Ascaphus truei***	Common	5	Common in Echo Lake basin in cool spring-fed perennial streams lacking Brook trout. Especially common at EVM, LVM, CAS, upper DPM and outlet of GSP. Conducted a mark-recapture study of this species in EVM and MVM from 2004 to 2005 (in preparation). Appears to have a minimum of three and possibly four larval cohorts based on size class distributions. Frogs also commonly seen in the main stream at Middle Siligo Meadows in 2007. Collected tissue samples.	Larvae Juvenile Adult
Pacific Treefrog ***Pseudacris regilla***	Common	5	Common in Echo lake and Siligo basins. Rare at RMM, Atlantis, and Billy Be Damned lake. In Echo Lake basin, this species had breeding sites at SMP, UVM, ECH, PTH, GSP and EDN every year 2003 -2007. The largest breeding aggregations were at SMP, with >200 of adult breeders present each spring depositing hundreds of egg masses. Adults rarely seen after breeding and assumed to migrate to surrounding talus fields. Collected tissue samples.	Egg Larvae Juvenile Adult
Western Toad ***Bufo boreas***	Regionally rare	2	Breeds at Deer lake but is rare everywhere else we conducted surveys. No individuals detected in Siligo basin and only two in Echo Lake basin. Three observations of solitary adults in 2003 (RMM, LVM and Deer Lake). In addition, One egg string detected at Deer lake in 2003. One adult observation below SMP in 2004.	Egg Adult
Reptilia				
Serpentes				
Rubber Boa ***Charina bottae***	Rarely detected	1	Observed one adult individual at night in Echo Lake basin on 10 Sep 2005 at 01:00. Our survey protocol was not designed to detect this species.	Adult
Western Rattlesnake ***Crotalus viridis***	Rarely detected	2	Observed one adult on Stony Ridge Trail swallowing a chipmunk (*Tamias* sp.) in 2004. Observed another adult at the ridge top due west of EDN in 2006. Our survey protocol was not designed to detect this terrestrial species, but we assume it's uncommon in the higher elevations.	Adult
Gopher Snake ***Pituophis catenifer***	Rarely detected	1	Observed one adult on Stony Ridge trail in 2004 ~ 500 m below RMM. Our survey protocol was not designed to detect this terrestrial species, but we assume it's rare at high elevations.	Adult
Lacertilia				
Alligator lizards ***Elgaria spp.***	Periodically observed	5	Found periodically in riparian areas during surveys in Echo Lake basin. Both species (*E. multicarinata* and *E. coerulea*) confirmed. Individuals seen at Echo lake, GSP, MOS, RMM and DPM.	Juvenile Adult
Western Skink ***Eumeces skiltonianus***	Periodically observed	2	Common on Stony Ridge trail up to mile three. None seen in areas of regular surveys. Our survey protocol was not designed to detect this terrestrial species.	Adult
Spiny lizards ***Sceloporous spp.***	Locally common	5	Common on Stony Ridge trail up to mile four, seen in Echo Lake basin on south facing slope above DPM. Our survey protocol was not designed to detect this terrestrial species but we assume it's locally common in lower elevations (<1500 m elevation) and in higher elevation south facing open slopes.	Juvenile Adult

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