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DISTRIBUTION AND HABITAT USE OF THE SANTA CLARA COUNTY
POPULATION OF RED-BELLIED NEWTS (*TARICHA RIVULARIS*)

A Thesis

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Master of Science

by

Joie de Leon

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DISTRIBUTION AND HABITAT USE OF THE SANTA CLARA COUNTY
POPULATION OF RED-BELLIED NEWTS (*TARICHA RIVULARIS*)

by

Joie de Leon

APPROVED FOR THE DEPARTMENT OF ENVIRONMENTAL STUDIES

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ABSTRACT

DISTRIBUTION AND HABITAT USE OF THE SANTA CLARA COUNTY
POPULATION OF RED-BELLIED NEWTS (*TARICHA RIVULARIS*)

by Joie de Leon

Anthropogenically-induced habitat loss and degradation have increased extinction rates in amphibians worldwide, yet little is known about many remaining populations. A disjunct population of Red-bellied Newt (*Taricha rivularis),* an endemic California species, was discovered 130 km south of its previously known range. Here I document the range and breeding phenology of this population and contrast its mesohabitat use with that of other sympatric newts. Surveys across two years suggest that the southern population of *T. rivularis* is confined to a 1 km segment of Stevens Creek, and the population follows an early-March to late-April migratory breeding pattern, similar to one documented northern population. Spatial analysis shows that *T. rivularis* aggregates only in Stevens Creek, likely dispersing through Twitty Creek. Breeding male *T. rivularis* are more associated with riffle and run mesohabitats when compared to pools, while *T. granulosa* and *T. torosa* tend to be more associated with woody debris cover types and cobble substrates. Female *T. rivularis* oviposition site selection is most influenced by large substrate size. The protection of large substrate and complex instream habitat in sensitive breeding reaches, as well as upland habitat along dispersal routes, should be an important consideration for land managers. Understanding the nuances of range, temporal behavior, and habitat needs for this disjunct population is critical to ensure the survival of this California Species of Special Concern.

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Finally, I thank my parents for their love and support in watching me learn about and chase after wildlife. To my partner in crime since the age of 19, Sovisit, thank you for your love, support, and encouragement as I strived toward my goals no matter how long it takes.

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One-third of all vertebrate species reside in the freshwater aquatic habitats that cover only 0.8% of the Earth's surface (Schneider et al. 2011). Among vertebrates, 41% of the ~8,300 identified amphibian species are threatened with extinction (IUCN 2021) The major threats to amphibian biodiversity decline are anthropogenic.

Amphibian species, including salamanders (Amphibia: Caudata), play critical ecological roles in their ecosystems (Davic and Welsh 2004). Salamanders provide ecosystem services that benefit their ecosystems and human society (Dudgeon et al. 2006). These services include pest regulation, indirectly supporting other species, and supporting medical research with unique adaptations (Hocking and Babbitt 2014). Salamanders also serve as "harbingers of environmental decay" or bioindicators (Vitt et al. 1990).

As amphibians, salamanders are among the most threatened group of vertebrates in the world (Alford and Richards 1999, IUCN 2021). Threats to salamanders are largely anthropogenic: global climate change, pollution, urbanization, habitat loss, and habitat degradation, introduced exotic species and disease (Alford and Richards 1999; Lannoo 2005; Dudgeon et al. 2006). Climate largely affects species distribution and potentially niche differentiation between closely related species (Corn 2005; Sutton et al. 2015)

The Red-bellied Newt (*Taricha rivularis*), a highly-specialized salamander species, is particularly vulnerable to habitat loss and fragmentation. Despite its status as a California Priority 2 Species of Special Concern, *T. rivularis* is poorly understood. In

2009, a single population of *T. rivularis* was discovered in the Santa Cruz Mountain Range in Santa Clara County. Data on this population could provide insights on how to protect the species throughout its range.

LITERATURE REVIEW

Niche Partitioning.—The competitive exclusion principle is the concept that if two species share the same niche or ecological role, then one of those species will drive the other to extinction. Conversely, when the two sympatric species occupy different niches, they are less likely to compete and can successfully co-exist (Hardin 1960). Niches can be partitioned differently depending on the ecological difference (food source, macro-habitat requirements, micro-habitat requirements, temporal requirement, etc.) of competing species (Schoener 1974). Recent studies have investigated the expected changes in niche partitioning of species in ecosystems that are most affected by global climate change (Corn 2005; Sutton et al. 2015).

Salamanders.—Amphibians are ectotherms comprising three orders of over 8,300 described species. Caecilians (order Gymnophiona), which make up 3% of described amphibian species, are specialized for burrowing, with no legs, reduced eyes, and an elongated body with grooves (Duellman and Treub 1994; IUCN 2021). Frogs (order Anura) make up 88% of described amphibian species, with elongated hind legs for jumping and no tails. Salamanders (order Caudata) make up 9% of described amphibian species, with elongated tails and four limbs of generally the same size (Duellman and Treub 1994; IUCN 2021). Salamanders are among the least understood amphibians due to their cryptic habits and nocturnal nature (Petranka 2010).

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Salamanders exhibit a variety of life histories that are either fully aquatic, fully terrestrial, or biphasic. Biphasic species undergo metamorphosis from an aquatic larva to a terrestrial or semiaquatic adult (Brown and Cai 2007; Dodd 2010; Duellman and Treub 1994). For all salamanders, unprotected gel-like eggs are deposited in locations with high humidity or moisture. Once hatched, salamander larvae with biphasic life histories grow until they metamorphose into juvenile salamanders (Duellman and Treub 1994). Unprotected egg masses and semi-permeable skin, combined with complex life histories, make many salamanders sensitive to changes in environmental conditions and ecological stress (Welsh and Ollivier 1998; Dudgeon et al. 2006).

Importance of Salamanders.—Most amphibian research has been conducted on the more abundant and obvious frog and toad species, which can be quite vocal. Salamanders are a quiet and cryptic group of amphibians that often lives underground between breeding seasons, making research difficult.

Ecosystem services are sometimes categorized into four groups: cultural services (education, recreation, therapeutic), provisioning services (raw materials, genetic resources, energy, food, medicinal resources), supporting services (primary production, soil production, nutrient cycling), and regulating services (pest control, waste decomposition, air, water purification) (Costanza et al. 1997). Salamanders provide ecosystem services that fall into each of these categories

Cultural Services.—Among amphibians, frogs have provided the majority of cultural ecosystem services due to their high visibility and abundance (Hocking and Babbitt 2014). Salamanders, like frogs, are animals that can be seen in zoos and are considered

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easy to care for in the pet trade. Their visibility in both zoos and the farmed pet trade provides value to children and families as a connection to nature and as pets. Salamanders have also appeared in a few children's stories and other novels such as Ray Bradbury's Fahrenheit 451 in which firefighters wore salamander symbols (Hocking and Babbitt 2014). In folklore and legend spread by both Pliny the Elder and Leonardo da Vinci, salamanders have been associated with fire (Hocking and Babbitt 2014; Wake and Koo 2018). The burning of logs gathered from the forest has contributed to the association of salamanders with fire: when gathered wood is burned, resident salamanders may emerge from the burning logs to escape the fire (Wake and Koo 2018).

Provisioning Services.— Salamanders and amphibians are also important for the advancement of medical technology and research. The ability to regenerate limbs and bones has been extensively studied (Song et al. 2010) and researchers are attempting to isolate the regenerative mechanisms to be used in modern medicine (Gupta 2016). However, Sessions and Wake (2020) hypothesize that regeneration may be unique to the salamander genome. Additionally, *Taricha* newts produce tetrodotoxin skin secretions, which may provide possible treatments in pain management, Parkinson's, Alzheimer's, and other neurological diseases (Lago et al. 2015).

Supporting Services.—Salamanders provide supporting services directly as prey, and indirectly as predators and dispersal agents (Hocking and Babbitt 2014). Salamanders are food sources to other amphibians, reptiles, fish, birds, mammals, and even large invertebrates (Duellman and Treub 1994; Petranka 2010). As predators in aquatic systems, salamanders help regulate tadpole abundance and feeding behavior, indirectly

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affecting algal and aquatic vegetation growth (Morin 1981). In terrestrial ecosystems, salamander predation indirectly reduces decomposition rates by regulating detritivore invertebrate populations on the forest floor (Wyman 1998). After metamorphosis and breeding, through their migration behavior between breeding waters and upland habitat, some salamanders facilitate dispersal and thus facilitate genetic diversity of unrelated species. Mole salamanders (Family: Ambystomatidae) can act as dispersal vectors for other species during migration by transporting small mollusks and the seeds of the bur-marigold between pools (Lowcock and Murphy 1990). Additionally, Ambystomid salamanders enhance genetic diversity across environments and between ponds by feeding on viable Colorado Fairy Shrimp (*Branchinecta coloradensis*) eggs in one pond and defecating in another (Bohonak and Whiteman 1999).

Regulating Services.—The majority of salamander species are predators, and they are often considered the dominant vertebrate predator in mature forests, including oak woodlands, redwood forests, and Douglas-fir forests (Burton and Likens 1975; Petranka et al. 1993; Welsh and Lind 1996; Davic and Welsh 2004). In mature forests, salamander density can be up to seven times greater than in younger forests (Petranka and Murray 2001). In many headwater streams, salamanders are the keystone aquatic predators because fish cannot traverse steep or rocky barriers (Wyman 1998; Brodman et al. 2003; Davic and Welsh 2004).

As keystone predators, salamanders can regulate invertebrate densities in aquatic and terrestrial environments (Davic 1991; Wyman 1998; Davic and Welsh 2004). Some Ambystoma species, for example, reduce mosquito larvae density in wetlands by 98%,

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reducing pests that can vector disease (Brodman et al. 2003; DuRant and Hopkins 2008).

Wyman (1998) found that the Red-backed Salamander (Plethodon cinerus) increased

detritus and carbon dynamics on the forest floor by feeding on terrestrial detritivores.

Ensatinas (*Ensatina eschscholtzii*) were also found to decrease invertebrate communities

and increase carbon capture of forest floors in the Santa Monica Mountains (Best and

Welsh 2014). Salamanders also regulate densities and distributions of other amphibian

species through competition (Hairston 1996; Walls and Williams 2001).

Bioindicators.—Salamanders can be bioindicators of environmental change and

stressors, ranging from anthropogenic toxin and sediment inputs to overall ecosystem

health (Welsh and Ollivier 1998; Simon et al. 2000; Townsend and Driscoll 2013).

Townsend and Driscoll (2013) found that the Red-backed Salamander (*P. cinereus*) is a

bioindicator for mercury within the forests of the northwestern United States. In

addition, ecosystem stress from human-induced sediment inputs can correlate directly

with amphibian abundance in redwood forests in California, where increased sediment

loads were shown to cause a decrease in amphibian species densities (Welsh and Ollivier

1998). Salamanders can also be utilized to assess the recovery of second-growth forest

systems after logging (Ashton et al, 2006). In North American forests, Welsh & Droege

(2001) suggest that plethodontid salamander populations are valuable to monitor

ecosystem integrity and biodiversity. Changes in plethodontid salamander populations

can be detected more quickly and accurately than other vertebrate species (such as

passerine birds, butterflies, small mammals or other amphibians) due to their complex life

history, unique physiology, and site fidelity.

Threats to Salamanders.— Salamanders are often overlooked because they are well hidden and are primarily observed during the rainy season (Petranka 2010). With the variety of ecosystem services that salamanders can provide and their inherent value as an indicator species, it is crucial to understand why they are declining rapidly.

Climate Change.—Anthropogenic climate change is considered a contributing factor for global amphibian species declines (Corn 2005; IUCN 2021). Changes in temperature and precipitation patterns can indirectly affect salamander populations by altering the timing of salamander emergence for breeding which, in turn, affects ecosystem community structure and competitive and predatory interactions (Beebee 1995; Carey and Alexander 2003). Precipitation pattern changes, such as too much or too little rain, can reduce aquatic amphibian populations through egg and larval mortality caused by unseasonable flood flows or earlier drying of pools and ponds (Alford and Richards 1999; Carey and Alexander 2003; Carey et al. 2005). Lack of rainfall may affect terrestrial salamanders through increasingly dry soils and loss of moist cover habitat, which can reduce prey populations and ultimately increase salamander mortality through desiccation (Donnelly and Crump 1998; Alford and Richards 1999).

Pollution.—Agricultural practices contribute to salamander habitat pollution through the use of nitrogen fertilizers (Baker and Waights 1994; Dudgeon et al. 2006). For example, nitrate pollution in aquatic systems reduces the growth rate and survival rate of larval Dwarf Newts (Triturus pygmaeus) (Ortiz-Santaliestra et al. 2007). In male Palmate Newts (Lissotriton helveticus), nitrate exposure reduced growth rates, breathing

capabilities, and altered the breeding attractiveness of males through the reduction of breeding scent production (Secondi et al. 2013).

Water acidification from air pollution caused female Dwarf Newts (*T. pygmaeus*) to fail to wrap deposited eggs with leaves of aquatic plants as protection, decreasing the survival of the egg mass (Ortiz-Santaliestra et al. 2007). In Two-lined Salamanders (*Eurycea bislineata*), mercury contamination disrupted locomotion ability and reduced the success rate of capturing prey (Burke et al. 2010). In urban riparian systems, impervious surfaces and vehicular toxins contribute to urban stream water pollution (Baker and Waights 1994; Davidson et al. 2001), which is correlated with a decrease in both Pacific Tree Frog (*Pseudacris regillia*) and California Newt (*Taricha torosa torosa*) populations (Riley et al. 2005).

Urbanization and Roads.—Urbanization and road infrastructure are also linked to pollution and sediment runoff and buildup in riparian systems (Davic and Welsh 2004). Welsh and Ollivier (1998) found that sediment inputs into streams at road construction sites cause amphibian densities to decline. Sediment fills interstitial spaces of stream substrate, which both amphibian species and their prey utilize for cover (Welsh and Ollivier 1998).

The life history patterns of many amphibian species require juvenile, sub-adult, and non-breeding salamanders to locate suitable upland habitat after metamorphosis and breeding (Trenham and Shaffer 2005). Direct road mortality is a significant cause of salamander decline in urban, suburban, and rural environments (Gibbs and Shriver 2005; Marsh et al. 2005; Sutherland et al. 2010). Many salamander species travel long

distances in terrestrial environments fragmented by roads, in some instances over 8 km (Twitty et al. 1967), making amphibians vulnerable to road mortality (Carr & Fahrig, 2001; Baldwin, Calhoun, & deMaynadier, 2006).

Habitat Loss and Degradation.—Habitat loss can occur with the installation of dams for urban water storage and hydroelectric power (Lind et al. 1996; Brode and Bury 1984). The effects to riparian habitat downstream of dams are well-documented (Lind et al. 1996; Brode and Bury 1984). Fluctuating flow regimes contribute to the decline of amphibian species directly by releasing unseasonably high flows and washing out deposited eggs or indirectly by changing sediment loads and allowing vegetation to narrow channels (Lind et al. 1996). Upstream of dams, riparian habitats are lost when converted into unstable lake habitat with fluctuating water levels (Brode and Bury 1984), causing loss of habitat essential for breeding, rearing, and cover or increases in predatory fish populations (Dudgeon et al. 2006; Brode and Bury 1984).

Agricultural land use changes and timber harvest have similar effects on riparian systems, degrading both aquatic and terrestrial habitat used by many salamanders. Clearing land for agricultural purposes or timber harvest increases sediment loads and air and water temperatures through tree cover loss (Petranka et al. 1993; Jackson et al. 2001). Timber harvest has caused a decline in the Tailed Frog (*Ascaphus* sp.), Olympic Salamander (*Rhyacotriton olympicus*), Siskiyou Mountains Salamander (*Plethodon stormi*), Eastern Newt (*Notophthalmus viridescens*), and Ambystomid salamanders (Bury 1968; Semlitsch 1998; Brode and Bury 1984). Ashton, Marks, & Welsh (2006) found

that timber harvest affected amphibian species richness and densities as much as 60 years after timber harvest.

Introduced Exotic Species and Disease.—The introduction of non-native predatory fish have been reported as the cause of population declines and local extirpations of many salamander species. Specifically, the introduction of Western Mosquitofish (*Gambusia affinis*) and Red Swamp Crayfish (*Procambarus clarki*) are linked to the decline of California Newt (*T. torosa*) in mountain streams in southern California (Gamradt and Kats 1996) and in urban California streams (Riley et al. 2005). An introduced pet tiger salamander species is reducing native populations of the threatened California Tiger Salamander (*Ambystoma californiese*) through competition and predation, as well as reducing native genetic diversity through hybridization (Riley et al. 2003).

The fungal pathogen known as chytrid fungus (*Batrachochytrium dendrobatidis*) has been linked to declines and extinction globally of many frog species and populations (AmphibiaWeb. 2011. An Overview of Chytridiomycosis. Available from https://amp hibiaweb.org/chytrid/chytridiomycosis.html [Accessed 5 July 2021]). In 2013, a new form of chytrid fungus that affects salamanders, *Batrachochytrium salamandrivorans* (*Bsal*), was described as an endemic species in Asia, and it is presumed to have been introduced to other localities by the amphibian pet trade (Martel et al. 2013; Grant et al. 2016). In a laboratory setting, *Bsal* was found to be lethal to salamanders in the United States, a global hotspot of salamander biodiversity (Wiens 2007; Grant et al. 2016), and Bsal was reported as the cause of unusual mortality of fire salamanders (*Salamandra salamandra*) in Europe (Martel et al. 2013).

Genus Taricha.—The genus *Taricha* (Family: Salamandridae) is a group of toxic

salamanders found in the western United States and Canada that consists of four species:

Rough-skinned Newt (*Taricha granulosa*), California or Coast Range Newt (*Taricha*

torosa), Sierra Newt (*Taricha sierrae*) and Red-bellied Newt *(Taricha rivularis)* (Twitty

1942; Twitty 1966; Stebbins 2003)*. Taricha* newts all secrete a specific tetrodotoxin or

neurotoxin, the same toxin found in pufferfish (Family: Tetraodontidae), that causes

paralysis when ingested or injected (Twitty 1937; Twitty 1966; Hague et al. 2016).

All *Taricha* ranges overlap, creating areas in which two, and sometimes three, of the

species are sympatric (Marks and Doyle 2005; Petranka 2010). During the breeding

season for each species, males develop smooth skin, long flattened tails, swollen vents,

and hardened toe tips or nuptial pads (Oliver and McCurdy 1974). Hybridization with

viable offspring can occur between *T. rivularis* and any other *Taricha* species through

artificial fertilization in a laboratory setting (Twitty 1966), but it is unlikely to occur

naturally due to species-specific mate attractants (Davis and Twitty 1964) and possibly

other aspects of niche differentiation. In riparian systems where ranges overlap, *T.*

granulosa and *T. torosa* breed in ponds or streams with slow-flowing water and pools. *T.*

rivularis, on the other hand*,* is considered an obligate stream breeder in its known

northern range, preferring streams with fast-flowing water (Twitty 1942).

Taricha granulosa.— Rough-skinned Newts (*T. granulosa*), the largest *Taricha*

newts, range between 12.5 and 22 cm total length (TL) (Taylor 1984; Neish 1971), with

light-brown to dark-brown dorsal coloration and a light-yellow to orange ventral. *T.*

granulosa eyes have yellow irises, and their eyelids are uniformly dark (Stebbins 2003).

T. granulosa occurs on the west coast of the United States, between southeastern

Alaska and San Francisco Bay Area, California, with two isolated (and possibly

introduced) populations in the Rocky Mountains of Idaho and Montana (Nussbaum and

Brodie 1971). Habitat requirements for *T. granulosa* include lakes, ephemeral ponds, or

slow-flowing sections of streams in forested mountains and foothills, and sometimes

grasslands (Petranka 2010). Although *T. granulosa* can inhabit many different

freshwater habitats and streams, it is rarely found in fast-flowing water (Petranka 2010).

T. granulosa oviposition occurs after mating, and females attach eggs singly to aquatic

vegetation, roots, or other detritus. Larvae in stream environments are secretive during

the day, hiding under vegetation and rocks, and they are generally found in warm

microhabitats and edges of the stream (Licht and Brown 1967).

Timing of migrations to and from breeding locations, as well as breeding, oviposition,

and larval metamorphosis, all vary throughout the range for this species, and breeding has

occurred in every month except November (Petranka 2010). In the Marion Lake

population, both males and females arrive mid-April and leave in mid-September (Neish

1971). The females in Vancouver Island migrate in the spring and remain until

September, while males remain in aquatic locations year-round (Oliver and McCurdy

1974). In high elevations, breeding usually occurs in summer and early autumn, but in

high-elevation California lakes, gravid females have been observed as late as mid-

October (Garber and Garber 1978; Oliver and McCurdy 1974). Conversely, peak

oviposition occurs in lower elevations of California in early March through early April

and has been documented as early as January (Twitty 1935). Egg incubation generally

lasts between 20 and 26 days to hatch (Petranka 2010). Timing for larvae to metamorphose ranges from 4 to 5 months in low elevations to almost a year in high-elevation cold lakes (Petranka 2010).

Taricha torosa.—California Newts (*T. torosa*) are also large salamanders, ranging from 12.5 to 20 cm TL (Riemer 1958). *T. torosa* is very similar to *T. granulosa* in appearance, making the two species difficult to distinguish in the field in areas where they co-occur. Key identifying characteristics include that *T. torosa* has vomerine teeth that form a Y-shape, lighter-colored lower eyelids, and eyes that extend beyond the margin of the head when observed from above (Stebbins 2003; Petranka 2010), as well as the behavioral difference that *T. granulosa* curls the tip of the tail into a coiled form when in an unken reflex or defense posture, while *T. torosa* will hold the tail tip straight (Riemer 1958).

T. torosa's range extends from northwestern California in Mendocino County to Southern California peninsular ranges in San Diego County, and it is found in a variety of habitats in forests, oak woodlands, chapparal, and grasslands from sea level to 2,000 m elevation. Adults breed in both pond and lake habitats and slow-flowing stream habitats (Petranka 2010).

Breeding usually lasts between 6 to 12 weeks, but the breeding season varies for *T. torosa* from December to early May, depending on location, and amplexing pairs have been observed as early as late September (Petranka 2010). In some locales, breeding can have two peaks, with pond-breeding occurring between December and January, while stream-breeding populations breed around March, when storms have subsided for the

season (Twitty 1942; Petranka 2010). The breeding period has even been found to differ

between a breeding stream and a pond that are 0.5 km apart (Marchetti and Hayes 2020).

After breeding, females oviposit spherical egg masses on vegetation, roots, and rock

in ponds or streams, and even directly onto the bottom of ponds (Twitty 1942; Stebbins

2003; Petranka 2010). Egg mass incubation varies with water temperature, with

estimates ranging from 52 days in west-central California to 14 to 21 days in southern

California (Mosher et al. 1964). Larvae usually transform during late-summer to early-

autumn (Riemer 1958) and disperse after metamorphosis.

The southern populations of *T. torosa,* from Monterey County to San Diego County,

are listed as a Priority 2 Species of Special Concern (Thomson et al. 2016). This

designation is due to extirpations and declining populations in areas with large or dense

human populations in which development, water diversions, and introduced predators

have caused habitat loss and degradation of both breeding habitat and terrestrial habitat

(Thomson et al. 2016). In streams in southern California, evidence suggests that

introduced crayfish and mosquitofish feed heavily on *T. torosa* egg masses, drastically

affecting local populations (Gamradt and Kats 1996). At present, northern populations of

T. torosa warrant no special conservation status on a regional or national level (Thomson

et al. 2016).

Taricha rivularis.—Red-bellied Newts (*T. rivularis*) can be described as a medium to

large stocky salamander with dark brown dorsal coloration and bright red ventral

coloration. As with all Taricha species, *T. rivularis* has rough granular skin, which

becomes smooth during the breeding season. The eyes of *T. rivularis* are a solid dark

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brown color, compared to the yellow and silver coloration of other *Taricha* species (Stebbins 2003). Research using individual markings has estimated that *T. rivularis* lives between 20 and 30 years (Twitty 1966; Hedgecock 1978).

The geographic range of *T. rivularis* includes Humboldt County, Lake County, Sonoma County Mendocino County, and newly as of 2009, Santa Clara County, California (Marks and Doyle 2005; Reilly et al. 2014). The new population of *T. rivularis* was discovered in the Santa Cruz Mountain Range approximately 130 km south of and across the San Francisco Bay from, the closest northern population. Although the southern population is not genetically dissimilar to the population in northern portion of its range, it is unclear if the population is introduced because low genetic diversity of the species prevents meaningful genetic comparisons (Kuchta and Tan 2006; Reilly et al. 2014). Based on genetic evidence from *T. rivularis* populations in the north, low variation may have been caused by rapid population expansion following a genetic bottleneck (Kuchta and Tan 2006; Reilly et al. 2014).

Habitat requirements of *T. rivularis* are poorly understood due to few investigations of the species. Although *T. rivularis* is generally found in the California coastal redwood belt, it is not restricted to coast redwood forests (Packer 1960; Stebbins 2003; Reilly et al. 2014). The southern population is found in a mixed evergreen forest within the Stevens Creek watershed with redwood forests nearby (Reilly et al. 2014). Aquatic habitat of *T. rivularis* for the northern population has been described as mountain brooks with clean, fast-flowing water (Twitty 1966; Stebbins 2003), however, no additional microhabitat requirements have been described. The terrestrial habitat has also not been described,

other than broad forest types and the presence of California bay laurel (pepperwood) (Twitty 1966; Stebbins 2003).

Homing migration and breeding ecology of *T. rivularis*, in contrast, were extensively studied in one "experimental stretch" of Pepperwood Creek in Sonoma County (Packer 1960; Davis and Twitty 1964; Twitty et al. 1964; Twitty 1966; Grant et al. 1968). In this location, Twitty and others (1964) observed the homing migration of breeding adult *T. rivularis* individuals returning to the original 15 meter (m) segment of stream after artificial displacement over 8 km away. Through artificial and surgical manipulation of the visual and olfactory senses, the authors further determined that *T. rivularis* uses smell as a homing mechanism to return to its natal stream segment (Twitty et al. 1964; Twitty 1966; Grant et al. 1968). Grant and others (1968) concluded that an individual *T. rivularis* imprints on the scent of its natal stream habitat just after metamorphosis.

Breeding migrations of northern *T. rivularis* populations start in late January and continue until May (Davis and Twitty 1964; Twitty et al. 1964; Twitty et al. 1964). Males arrive at the stream first, and, upon the arrival of the first females, breeding congregations form, and mating begins (Davis and Twitty 1964). After mating, females travel to areas of fast-flowing, well-oxygenated water and deposit egg clusters to the bottoms or edges of large rocks (Davis and Twitty 1964). In some locations where adult *T. rivularis* densities are high, up to 70 egg masses have been found on the bottom of a small stone (Twitty 1935; Twitty 1942). When the breeding season is complete, individuals leave the stream and find refuge underground until the first heavy winter rains

stimulate individuals to emerge to forage for insects and other invertebrates (Twitty 1966).

In a laboratory setting, egg incubation lasts 16 to 20 days at 23 degrees Celsius and 30 to 34 days at 15 degrees Celsius, and the larval stage of *T. rivularis* lasts 4 to 6 months (Licht and Brown 1967). Although larvae are found in pools, specific adaptations such as a streamlined body shape with more developed limbs and reduced balancers allow the larvae to survive the mountain brook habitat (Davis and Twitty 1964; Twitty 1966; Licht and Brown 1967). After metamorphosis, juveniles migrate upland to find underground shelter, where they remain until they reach maturity at approximately five years (Twitty 1955; Twitty 1966).

T. rivularis is a California endemic species that is an obligate stream-breeding and -rearing salamander that utilizes habitats susceptible to anthropogenic habitat loss and degradation. Much of the habitat in the *T. rivularis* range is threatened by timber harvest, agricultural practices, and urbanization (Reilly et al. 2014; Thomson et al. 2016). Because *T. rivularis* is such a poorly-studied species, more research is needed to protect critical habitat components and provide for species recovery (Thomson et al. 2016).

No habitat research has not been conducted on the Santa Clara County *T. rivularis* population (Reilly et al. 2014) let alone on the species throughout its range. *T. rivularis* is a long lived specialized salamanders with strong site fidelity (Twitty et al. 1964; Hedgecock 1978), the Santa Clara Population of *T. rivularis* has the potential to be a bioindicator of environmental and ecological stress from anthropogenic influences (Welsh and Ollivier 1998). The habitat of the disjunct Santa Clara County population

may serve as a habitat refugium in the face of unknown future climate scenarios (Lesica and Allendorf 1995; Reilly et al. 2014).

This study assesses the breeding range, timing and the aquatic mesohabitat preferences of this important Santa Clara County population of *T. rivularis* in the context of its sympatric congeners. Information provided is intended to aid resource managers in protecting this disjunct population and a California Species of Special Concern along with *T. granulosa* and *T. torosa* in this unique ecosystem.

OBJECTIVES AND RESEARCH QUESTIONS

The objective of this research was to gather distribution and habitat data on the disjunct Santa Clara County population of Red-bellied Newts (*T. rivularis*). Specifically, I answer the questions: Where is the southern population found? In the context of sympatry with rough-skinned newts (*T. granulosa*) and California Newts (*T. torosa*) what are the phenology and mesohabitat preferences of males during the breeding season and oviposition site selection of females?

Research Questions.—

RQ1: Southern population range: What is the current range of the southern population of *T. rivularis*?

RQ2: Southern population breeding phenology

    a: What is the timing of breeding migrations of the southern population *T. rivularis*, as compared with sympatric newts and other salamanders encountered?

    b: How does spatial aggregation of males of the southern population of *T. rivularis* vary throughout its breeding season in each occupied stream?

RQ3: Male habitat use and availability

    c: How does mesohabitat availability compare between *T. rivularis* breeding versus

        non-breeding streams?

    d: How does *Taricha* newt mesohabitat use compare with available mesohabitats in

        T. rivularis-occupied reaches?

    e: How do aquatic mesohabitat, substrate and cover preferences of adult male *T.*

        rivularis differ from these preferences for sympatric congeners?

RQ4: How does female *T. rivularis* habitat selection for oviposition site differ from

interspersed random sites within Stevens Creek?

INTRODUCTION

Amphibians are among the most threatened group of vertebrates in the world, and global population declines are well documented (Wake 1991; Alford and Richards 1999; IUCN 2021). Threats are largely anthropogenic, including global climate change, pollution, urbanization, habitat loss, habitat degradation, and introduced exotic species and disease (Dudgeon et al. 2006). Many amphibian population declines are not attributed to a single factor but rather a combination of variables that are not always identified; many field studies only focus on single factors (Davidson and Knapp 2007). Lack of understanding of the multifactorial causes of population declines and limited knowledge of life history patterns can impair conservationists' ability to protect a species (Bishop et al. 2012).

The Red-bellied Newt (*Taricha rivularis*), a highly specialized salamander species, is particularly vulnerable. Despite its status as a California Priority 2 Species of Special Concern, data on *T. rivularis* are lacking. Most knowledge of the species comes from one extensively studied population in an "experimental stretch" of Pepperwood Creek in Sonoma County, California, USA (Packer 1960; Davis and Twitty 1964; Twitty et al. 1964; Twitty 1966; Grant et al. 1968). In 2009, a new population of *T. rivularis* was discovered in the Santa Cruz Mountain Range in Santa Clara County, California, USA. Data from this population will provide insights on how to protect the species throughout its range.

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T. *rivularis* is a medium to large stocky salamander that occurs from Humboldt
County, California, USA to Sonoma County, California, USA and, as of 2009, in Santa
Clara County, California, USA (Marks and Doyle 2005; Reilly et al. 2014). Habitat
requirements of *T. rivularis* are poorly understood. Victor Twitty (1966) simply
described the terrestrial habitat of *T. rivularis* as broad forest types with the presence of
"Pepperwood" or California Bay Laurel (*Umbellularia californica*). However, the species
is generally found in, but not restricted to, the California Coast Redwood (*Sequoia
sempervirens*) belt (Packer 1960; Stebbins 2003; Reilly et al. 2014). Aquatic habitat of *T.
rivularis* for the northern population has been described as mountain brooks with clean,
fast-moving water (Twitty 1966; Stebbins 2003); however, no additional microhabitat
requirements have been described.

Breeding ecology and migrations of *T. rivularis*, in contrast, were extensively studied
in an experimental stretch of Pepperwood Creek (Packer 1960; Davis and Twitty 1964;
Twitty et al. 1964; Twitty 1966; Grant et al. 1968). Twitty and others (1964) documented
and experimented with the mechanisms of homing migration of *T. rivularis* individuals
returning to the original 15 m segment of stream after artificial displacement over 8 km
away. Breeding migrations of northern *T. rivularis* populations begin in late January,
arriving in the stream around late February to early March after heavy storms subside,
and continue until May (Davis and Twitty 1964; Twitty et al. 1964; Twitty et al. 1964).
Males arrive at the stream first and, upon the arrival of the first females, breeding
congregations form, and mating begins (Davis and Twitty 1964). After mating, females
travel to areas of fast-flowing, well-oxygenated water and deposit egg clusters to the

bottoms or edges of large rocks (Davis and Twitty 1964). In some locations where adult

T. rivularis densities are high, up to 70 egg masses have been found on the bottom of a

single stone (Twitty 1935; Twitty 1942). When the breeding season is complete,

individuals leave the stream and find refuge underground until the first heavy winter rains

stimulate individuals to emerge to forage for insects and other invertebrates (Twitty

1966).

    Taricha rivularis is an obligate stream-breeding and -rearing salamander that utilizes

habitats susceptible to anthropogenic habitat loss and degradation (Twitty 1966; Marks

and Doyle 2005; Petranka 2010). Habitat loss due to land use changes, logging practices,

and human road expansion degrades stream habitat with pollution and sediment inputs

and fragments migratory habitat (Corn and Bury 1989; Jackson et al. 2001; Peterman et

al. 2008). Much of the habitat in the *T. rivularis* range is threatened by timber harvest,

agricultural practices, and urbanization (Reilly et al. 2014; Thomson et al. 2016).

Because *T. rivularis* is such a poorly-studied species, more research is needed to protect

critical habitat components and provide for species conservation (Thomson et al. 2016).

    No habitat research has previously been conducted on the Santa Clara County *T.*

rivularis population in the upper Stevens Creek headwater tributaries (Reilly et al. 2014).

As specialized riparian forest salamanders with long life spans and strong site fidelity

(Twitty et al. 1964; Hedgecock 1978), this population of *T. rivularis* has the potential to

be a bioindicator of environmental and ecological stress from anthropogenic influences

(Welsh and Ollivier 1998). In addition, the habitat of the disjunct Santa Clara County

population of *T. rivularis,* may serve as a habitat refugium in the face of unknown future climate scenarios (Lesica and Allendorf 1995; Reilly et al. 2014).

In addition, Santa Clara County harbors three of the *Taricha* species: *T. rivularis, T. granulosa* and *T. torosa*. All *Taricha* ranges overlap, creating areas in which two, and sometimes three, of the species are sympatric (Figure 1) (Marks and Doyle 2005; Petranka 2010). In riparian systems where ranges overlap, *T. granulosa* and *T. torosa* breed in ponds or streams with slow-moving water and pools. *T. rivularis,* on the other hand*,* is considered an obligate stream breeder in its known northern range, preferring streams with fast-flowing water (Twitty 1942). Minimal investigatory research has looked into how these three species interact within an ecosystem are lacking.

The largest of the *Taricha* salamanders is the Rough-skinned Newt (*T. granulosa*) (Taylor 1984; Neish 1971) that ranges geographically from southeastern Alaska to the San Francisco Bay Area, California, with two isolated (and possibly introduced) populations in the Rocky Mountains of Idaho and Montana (Nussbaum and Brodie 1971). Habitat requirements for *T. granulosa* include lakes, ephemeral ponds or slow-flowing sections of streams in forested mountains and foothills, and sometimes grasslands; rarely is *T. granulosa* found in fast-flowing waters (Petranka 2010). Timing of migration, breeding, oviposition and larval metamorphosis vary throughout the range for this species. Peak oviposition occurs in lower elevations of California in early March through early April, and oviposition has been documented as early as January (Twitty 1935).
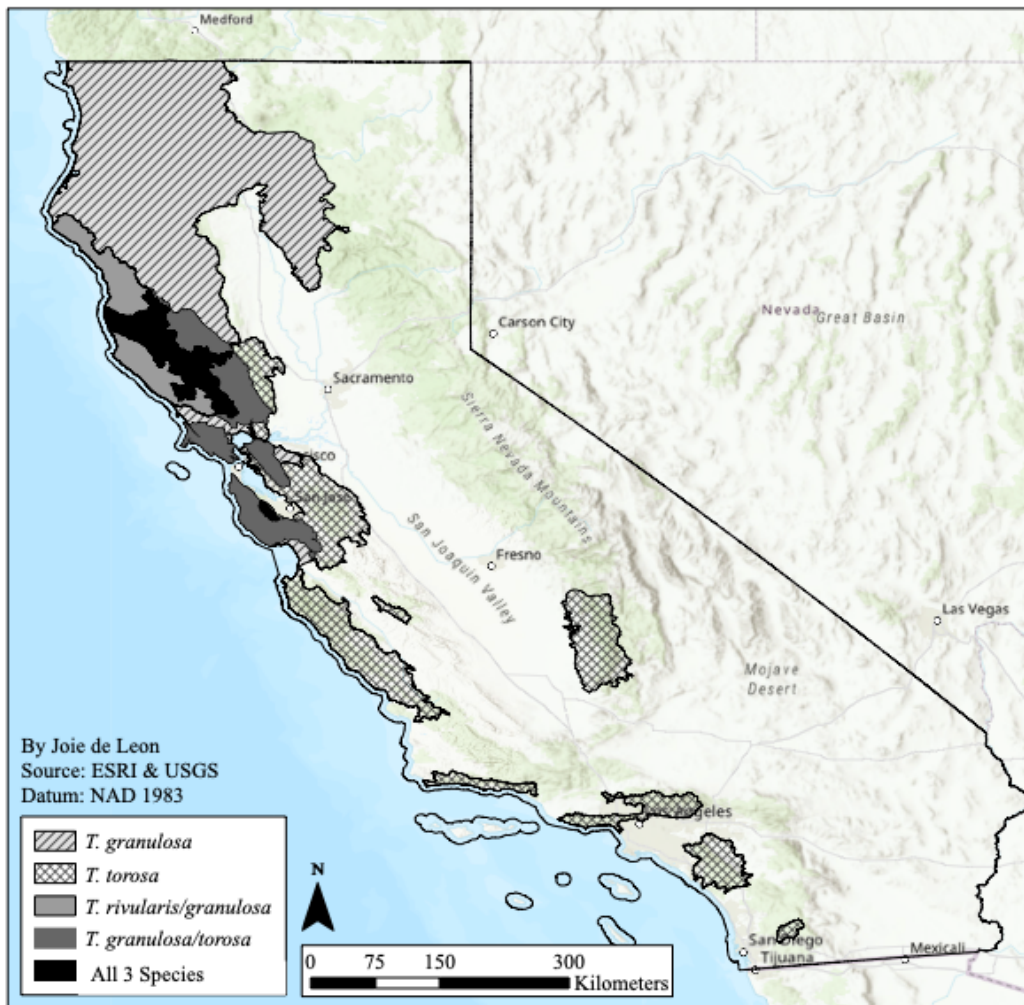
Figure 1. California ranges of *T. rivularis*, *T. granulosa* (diagonal lines), and *T. torosa* (hatched lines) locations where ranges overlap. The entirety of *T. rivularis* range is shared with *T. granulosa* (light gray).

California Newts (*T. torosa)* are also large salamanders, very similar to *T. granulosa* in appearance, making the two species difficult to distinguish in the field in areas where they co-occur. *T. torosa* ranges from northwestern California in Mendocino County to Southern California peninsular ranges in San Diego County. The southern populations of *T. torosa,* from Monterey County to San Diego County, are listed as a Priority 2 Species of Special Concern (Marchetti & Hayes, 2020). This designation is due to extirpations

and declining populations in areas with large or dense human populations in which development, water diversions, and introduced predators have caused habitat loss and degradation of both breeding habitat and terrestrial habitat (Thomson et al. 2016).

Habitat requirements include lakes, ponds or slow-flowing sections of streams in forests, oak woodlands, chapparal, and grassland (Petranka 2010). Southern populations have been found depositing eggs in faster-flowing streams (Gamradt and Kats 1997). The breeding season varies from December to early May, depending on location (Petranka 2010). In some locales, breeding can have two peaks, with pond-breeding occurring between December and January, while stream-breeding populations breed around March, when storms have subsided for the season (Twitty 1942; Petranka 2010). The breeding period has even been found to vary between a breeding stream and a pond 0.5 km apart (Marchetti and Hayes 2020).

This study assesses and attempts to fill some knowledge gaps on *T. rivularis* and the interactions with sympatric newts, *T. granulosa* and *T. torosa*. The distribution, breeding range, timing of breeding migrations and the aquatic mesohabitat preferences of this Santa Clara County population of *T. rivularis* in the context of its sympatric congeners. Information provided is intended to aid resource managers in protecting this disjunct population of a California Species of Special Concern, along with *T. granulosa* and *T. torosa,* in this unique ecosystem.

MATERIALS AND METHODS

Study Area.—I conducted this study in Upper Stevens Creek County Park and Midpeninsula Regional Open Space District (MROSD) park properties, including Monte

Bello Open Space Preserve, Skyline Ridge Open Space Preserve, and Long Ridge Open

Space Preserve. These locations are within the Santa Cruz Mountain Range in Santa

Clara and San Mateo Counties, California, USA, approximately 58 km south of San

Francisco and 20 km west of San Jose (Figure 2).
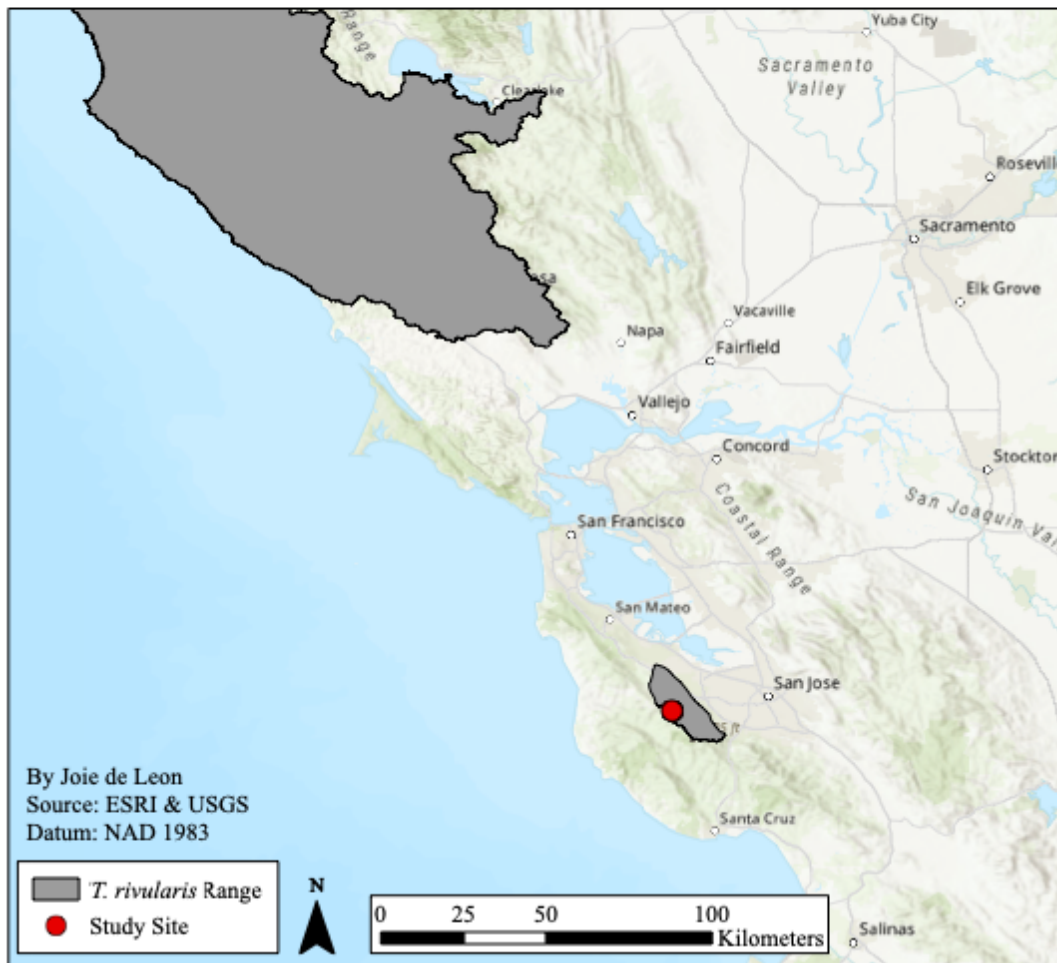
Figure 2. Map of *T. rivularis* range around the San Francisco Bay Area in gray. The red dot represents our study site in the Stevens Creek watershed in Santa Clara County.

In 2018, I surveyed the publicly accessible tributaries of Upper Stevens Creek,

including a tributary colloquially named by MROSD Staff as "Twitty" Creek; the

adjacent headwaters of the upper San Gregorio Creek watershed of Lambert Creek and its tributaries; and a small portion of Peter's Creek in the headwaters of the upper Pescadero Creek watershed. Stream sampling was limited to MROSD property and Santa Clara County Parks Upper Stevens Creek Park, as sampling on private property was not possible.

I reduced the study area in 2019 to only include the two stream reaches within the Stevens Creek Watershed in which *T. rivularis* was found in the 2018 surveys: Stevens Creek Reach 4 and Twitty Creek.

Dense mixed evergreen Douglas-fir forest with interspersed redwoods surrounds much of Upper Stevens Creek watershed above the reservoir. Oak-woodland forest and nearby grasslands that have been historically used for cattle grazing are also present (MROSD. 2016. Monte Bello Preserve. Available from https://www.openspace.org/preserves/monte-bello [Accessed 5 July 2021]). The Stevens Creek watershed drains approximately 75 km^2 into the San Francisco Bay Estuary, just north of Moffett Field Naval Air Station. Stevens Creek begins at Black Mountain in the Monte Bello Open Space Preserve and passes through Upper Stevens Creek County Park, Santa Clara County. One major impoundment, Stevens Creek Reservoir, provides winter runoff storage for the Santa Clara Valley Water District and maintains a wet channel to preserve federally endangered steelhead (Leidy et al. 2005).

Both Upper Stevens Creek and Twitty Creek are well-entrenched channels, with some areas of sinuosity and less entrenched channels. Boulder and cobble are the dominant substrates, but gravel and sand are also interspersed throughout the study area. The

majority of the channels surveyed are densely canopied with Douglas-fir (*Pseudotsuga menziesii*), California Buckeye (*Aesculus californica*), Pacific Madrone (*Arbutus menziesii*), White Alder (*Alnus rhombifolia*), and willows (*Salix* spp.), with Coast Redwood (*Sequoia sempervirens*), Coast-live Oak (*Quercus agrifolia*), Big-leaf Maple (*Acer macrophyllum*), and Tan-oak (*Notholithocarpus densiflorus*) also present. Sword Fern (*Polystichum minunitum*), Poison Oak (*Toxicodendron diversilobum*), California Stinging Nettle (*Urtica dioica*), Trailing Blackberry (*Rubus ursinus*), Thimbleberry (*Rubus parviflorus*), Western Coltsfoot (*Petasites palmatus*), and many other herbaceous groundcover species are present along banks and flood plains of the less-entrenched areas of stream.

Many other wildlife species also use the watershed. The mesocarnivores, such as the Gray Fox (*Urocyon cinereoargenteus*), Bobcat (*Lynx rufus*) and raptors, are not threats to *Taricha* due to its tetrodotoxin (Twitty 1937; Twitty 1966; Hanifin 2010; Vaelli et al. 2020). Other mammals, including the American Badger (*Taxidea taxus*), the Dusky-footed Woodrat (*Neotoma fuscipes*) and other burrowing mammals, potentially create terrestrial refugia in the form of burrows for amphibious species (Vestal 1938; Trenham 2001; Trenham and Shaffer 2005; Innes et al. 2007). Multiple snake species, including the Common Garter Snake (*Thamnophis atratus*) and its sub-species, the Santa Cruz Garter Snake (*T. a. atratus*), are present near Stevens Creek (Stebbins 2003). The Common Garter Snake and the Santa Cruz Garter Snake are among the few known predators capable of surviving the *Taricha* tetrodotoxin (Brodie 1968; Williams et al. 2010). A few fish species, including Rainbow Trout (*Oncorhynchus mykiss*) (historically

Steelhead Trout, prior to building Stevens Creek Reservoir) use the Stevens Creek

watershed (Leidy et al. 2005; Jerry Smith unpubl. report). In addition to the *Taricha*

newts, other salamanders in the watershed include the Pacific Giant Salamander

(*Dicamptodon ensatus*) and the terrestrial California Slender Salamander (*Batrachoseps*

attenuatus), Ensatina (*Ensatin eschscholtzii*), Arboreal Salamander (*Aneides lugubris*)

and Santa Cruz Black Salamander (*A. flavpunctatus*) (Stebbins 2003).

 Study Design.—I conducted visual encounter surveys in 2018 to identify stream

reaches within all the watersheds sampled that supported detectable populations of *T.*

rivularis. Visual encounter surveys record the presence of *T. rivularis*, but they do not

determine absence. From March to April 2018, I conducted 12 timed visual encounter

surveys in tributaries and streams adjacent to Twitty Creek in the Stevens Creek

watershed and Pescadero and San Gregorio watersheds.

 In 2019, I conducted visual encounter surveys for all newts and salamanders from

March to May 2019, for a total of nine surveys, four in Twitty Creek and five in Stevens

Creek. Surveys began later in the season than in 2018 due to heavy storms causing high

flows and turbidity in February and early March (Figure 3).

 For each *T. rivularis* individual encountered on each survey date, I recorded the GPS

coordinate to evaluate intraspecific distributions. I used aggregated distributions as an

indicator of active breeding activity habitat within the occupied range (Packer 1963;

Twitty 1966). In addition to GPS location, I recorded the sex and age class of each

individual.
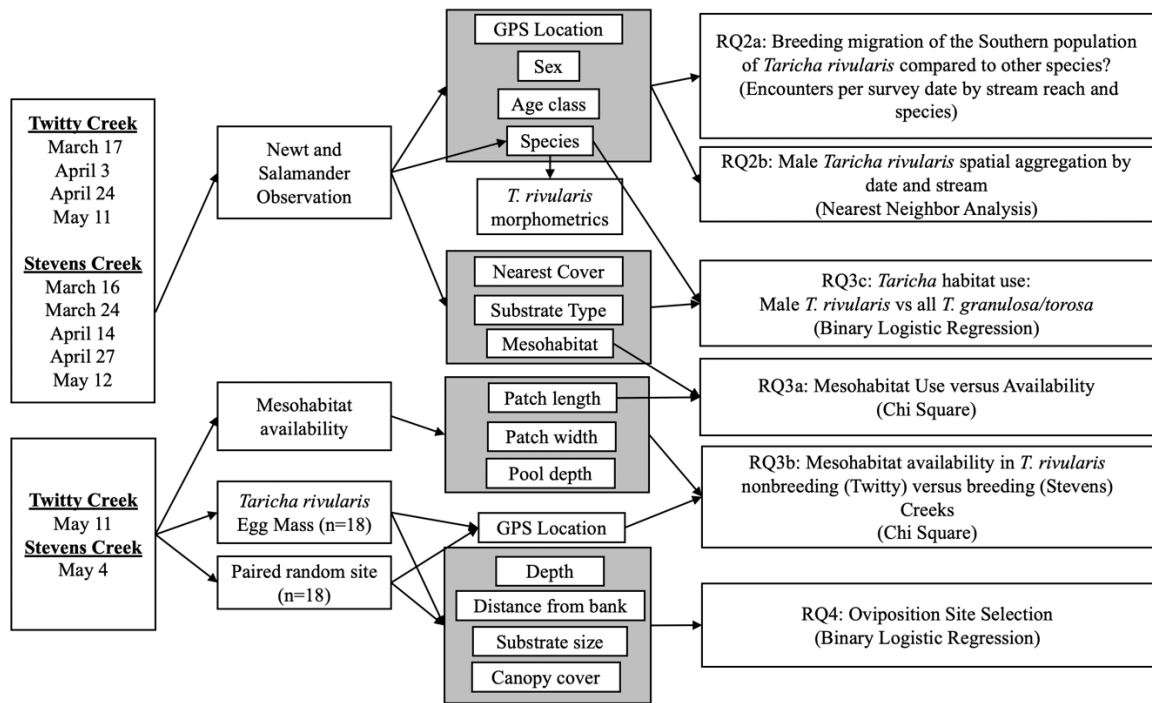
Figure 3. Study design for 2019 surveys.

I mapped the overall mesohabitat data for Stevens and Twitty Creeks to compare the
relative availability of different mesohabitats across the two stream reaches. I
characterized aquatic mesohabitat type, substrate type, and nearest cover type preferences
for breeding adults of all *Taricha* species as I encountered them in the field. I then
compared the overall percentages of mesohabitats used by each species with available
mesohabitats to assess the selectiveness of each species. I recorded mesohabitat,
substrate and cover preferences of each *Taricha* individual observed during 2019 surveys
by date and location to assess differences in habitat preference between *T. rivularis* and
sympatric congeners.

Once breeding was completed and all adult *T. rivularis* had left the stream, I
conducted egg mass surveys. For each oviposition site located, I randomly selected a

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paired unoccupied site within ten possible oviposition sites. I collected data on habitat

characteristics for all sites where I detected egg masses and for paired randomly chosen

sites to characterize breeding female habitat selectivity.

   Data Collection.—For the initial 2018 surveys, two to four observers started from a

predetermined accessible location and walked either upstream or downstream until the

end of the planned stretch or until the stream was no longer accessible due to property

ownership, personal safety in accessing the area, or physical ability to walk along the

channel. Observers actively searched for *T. rivularis* or any other newt or salamander

species within the stream, along the banks, and in any location within a meter of the

bank.

   I did not handle pairs and groups found in amplexus, and therefore did not sex or

measure, to avoid disrupting reproductive behaviors. For all other *T. rivularis*

encountered, I captured (with wet hands), identified, measured the total length (TL) and

snout-vent length (SVL), using a metric ruler to the nearest millimeter (mm), weighed to

the nearest gram with a Pesola spring scale, and recorded the age class (adult or juvenile)

and sex of each individual. Breeding males have a swollen vent with a black bar across

the vent, presence of smooth skin, and a long flattened tail (Twitty 1942; Twitty 1966).

After collecting data, I immediately released the individual in the same location in which

it was captured and recorded the GPS coordinates. For *T. granulosa* or *T. torosa,*

observers captured, identified, and then immediately released them at the location of

capture. I did not capture GPS coordinates for *T. granulosa* or *T. torosa.* In many

instances, specific morphological separation of *T. granulosa* versus *T. torosa* was not

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possible due to their similar biometrics, so I recorded those individuals as indeterminate *T. granulosa/torosa.* I also recorded GPS coordinates of *Dicamptodon ensatus* encountered but did not handle individuals.

In 2019, I conducted surveys again with two to four observers walking upstream along the channel while actively searching for any newt or salamander species. As in 2018, observers captured with wet hands and identified, measured for TL and SVL, and sexed *T. rivularis* adults (not in amplexus) and juveniles. In Stevens Creek, due to the large numbers of *T. rivularis* individuals I encountered, I only measured and recorded every tenth *T. rivularis* observation measured and recorded. I captured the entire group present at each tenth observation and individuals I sexed and measured as described above. I recorded GPS coordinates for each *T. rivularis* and *D. ensatus* observed. I captured *T. granulosa* and *T. torosa* for identification purposes only.

I recorded mesohabitat type, substrate type, and nearest cover type for each salamander observed (see Figure 3). I defined instream mesohabitats as pool, run, riffle, or cascade (Hawkins et al. 1993), and bank is also used for individuals that I observed outside of the wetted channel. Pool is defined as deep areas of slow-flowing water with low gradient and fine sediment. A run is defined as non-turbulent fast-flowing water with a low gradient. A riffle is defined as turbulent fast-flowing water with a steeper gradient and coarser sediment. Cascade is defined as turbulent fast-flowing water with a steep gradient and larger boulders (Hawkins et al. 1993). Substrate type is identified as: silt or organic matter; sand; gravel or pebble (2–64 mm); cobble (64–256 mm); boulder (>256 mm); or bedrock (Bury and Corn 1991). Nearest cover type is defined as large woody

debris, overhanging vegetation, water depth, rocks, boulders, and loose streambed material.

I conducted surveys to assess overall mesohabitat availability on 4 May 2019 in Stevens Creek and on 11 May 2019 in Twitty Creek, starting at the Twitty-Stevens confluence, as for the visual encounter surveys. I measured with a transect tape and recorded by mesohabitat type the length and width of each mesohabitat patch in each stream reach. I determined the maximum depth of each pool using a metric ruler.

I conducted egg mass surveys on these two dates as well, 4 May 2019 in Stevens Creek and on 11 May 2019 in Twitty Creek. While walking upstream, I surveyed by reaching into interstitial spaces of cobbles and boulders while feeling gently for egg masses. I never moved substrate during the search process to prevent any disturbance or dislodgement of egg masses. Because newts can fit in much smaller spaces than the hands of surveyors, it is assumed that the search for egg masses was not exhaustive. Adjacent to each site with at least one egg mass, I selected a paired unoccupied site using a random number generator to move between one and ten potential oviposition sites either upstream or downstream of the egg mass location.

At each egg mass site and each paired unoccupied site, I collected the following data: number of egg masses; egg mass depth; position in stream (left, center, or right when looking downstream); distance from both left and right bank; attached substrate type (cobble, boulder, woody debris); attached substrate size (cm^2); mesohabitat type (pool, run, riffle); and canopy cover (Forestry Suppliers Spherical Crown Densiometer).

Data Analysis.—I used ArcGIS Pro 2.7 (ESRI, Redlands, California USA) to document the presence of *Taricha rivularis* in its southern range. I assessed whether the distribution of observed *T. rivularis* was clustered, dispersed, or randomly distributed on each date in each location sampled using the average nearest neighbor (ANN) tool in ArcGIS Pro 2.7. The ANN tool tests whether the average distance between a set of points is greater or less than a hypothetical random distribution (the null hypothesis) or indistinguishable from it (the alternate hypothesis). If $P > 0.05$, the null hypothesis is accepted, and the points are considered randomly distributed. If $P < 0.05$ and the z-score is < -1.96 or $> +1.96$, the null hypothesis is rejected, and the nearest neighbor ratio (NNR) is used to assess aggregation. The NNR is the observed mean distance / expected mean distance in a given area. If NNR > 1.0, the distribution is over-dispersed; if NNR < 1.0, the distribution is clustered or aggregated (Andy Mitchell 2005). I ran ANN analysis across all survey dates combined for each creek and each survey date and each creek separately.

I recorded by date all encounters of *T. rivularis* individuals and other newts and salamanders to describe seasonal movements of *Taricha rivularis* and sympatric salamander species. Due to the high variability in time needed to process and record data depending on the numbers of *T. rivularis* encountered, I utilized total catch per survey date as the unit of measure rather than catch-per-unit-effort.

I summarized available mesohabitat percentages for each surveyed reach and ran a chi-square goodness-of-fit test in R (R Development Core Team 2017) to assess differences among percentages of each mesohabitat type in each occupied stream.

I summarized percent habitat use data for each newt or salamander species and compared the mesohabitat-use percentages for the three *Taricha* species versus the available habitat percentages for each stream reach using a chi-squared goodness-of-fit test. I excluded *D. ensatus* from the comparison due to low numbers.

In preparation for inferential analysis, I grouped or removed species and habitat to strengthen statistical power. I excluded observations in which the mesohabitat was described as "bank" or "cascade" due to low numbers. I removed *T. torosa* from the analysis due to the low numbers of observations in Stevens Creek and the uncertain specific identification for some *T. granulosa/torosa* individuals. I combined low-frequency habitat variables as follows: cover types of "boulder," "cobble," and "bedrock cracks" combined into "interstitial spaces." Cover types "large woody debris," "small woody debris," "woody debris," "organic matter" and "roots" combined into a single cover type: "Organic Matter/Vegetation." Substrate types "silt/organic matter," "vegetation," "woody debris" and "roots" combined into the substrate type: "Silt/Organic Matter." Finally, I used only variables within Stevens Creek due to breeding occurring only within Stevens Creek.

I contrasted *T. rivularis* adult male breeding habitat parameters with those of sympatric congeners using a binary logistic regression run through the GLM function in R (R Development Core Team 2017) with species (*T. rivularis* versus *T. granulosa)* as the binary dependent variable. Predictor variables included are mesohabitat (pool, riffle, and run), substrate (boulder/bedrock, cobble, gravel, sand, and silt/organic matter), and

nearest cover type (interstitial spaces, undercut bank, water depth, woody debris, organic matter/vegetation).

The initial full model that included all habitat variables was reduced by using the dredge, or automated model selection, function in the MuMIn package (Kamil 2020). MuMIn function runs every possible combination of variables and identifies the best fitting model using the AICc and deltaAIC (Burnham and Anderson 2002; Kamil 2020).

To predict the odds that the *Taricha* newt is either *T. rivularis* or *T. granulosa*, I used the binary logistic regression based on the individual's presence in or near a specific habitat variable. In the analysis, one can infer from the coefficient estimate ß, how much proximity to a specific habitat variable increases or decreases the odds of a newt being a *T. rivularis* on a log scale; standard error (SE); *z* is the Wald's test value, or how many standard deviations the ß values are away from 0 on a standard normal curve; Odds Ratio is the exponentiation of ß. Both ß and the odds ratios are used to interpret the strength of associations among the habitat variables and the *Taricha* species in Stevens and Twitty Creeks.

For the mesohabitat category, the binary logistic regression analysis used "pool" as the reference variable, the habitat variable against which all the other habitat variables in the category are compared. For substrate, the reference variable was "boulder." For cover type, the reference variable was "interstitial spaces."

I also used a binary logistic regression model to identify associations among habitat variables and the presence/absence of a *T. rivularis* oviposition site. The predictor variables are mesohabitat (pool, riffle, and run), attached substrate (boulder, cobble, and

wood), substrate size (cm^3), depth (m), distance from bank (m), and canopy cover. I

determined the best possible model as described for adults above. The initial binary

logistic regression using the GLM function with all the measured and categorical

variables, followed by a dredge analysis with automated model selection, determined that

substrate size alone was the best predictor of the presence/absence of a *T. rivularis*

oviposition site. I ran the final binary logistic regression model using only substrate size

as the predictor. To confirm the significance of the model, I ran a Mann-Whitney U.

<div align="center">

RESULTS

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Range.—In 2018, I recorded a total of 110 *T. rivularis* individuals and one pair in

amplexus between 7 March 2018 and 29 April 2018 in Stevens Creek Reach 4, Twitty

Creek, and an unnamed tributary south of the Twitty-Stevens confluence (Table 1). Of

the 110 observed individuals, I captured 57 adult males (SVL = 68.7 mm ± 0.8 mm;

range, 51–89 mm) and eight juveniles (SVL = 27.0 mm ± 1.0 mm; range, 23–32 mm). I

found no *T. rivularis* individuals during surveys in Lambert Creek, in the adjacent

watersheds, or in the remaining Stevens Creek reaches or tributaries of Indian Creek, Bay

Creek, Gold Mine Creek, and four unnamed tributaries (Table 1).

Table 1. *T. rivularis* Observations in Each of the Survey Locations for 2018.

Date	Location	Adult	Juvenile
7-Mar	Twitty Creek	15	7
12-Mar	Lambert Tributary	0	0
18-Mar	Lambert Creek (Lower)	0	0
19-Mar	Lambert Creek (Upper)	0	0
29-Mar	Twitty Creek	9	3
31-Mar	Indian Creek & Stevens Reach 7	0	0
4-Apr	Unnamed Tributary & Twitty Confluence	3	1
11-Apr	Unnamed Tributary (2) & Stevens Reach 1	0	0
16-Apr	Unnamed Tributary & Stevens Reach 2	1	0
18-Apr	Stevens Reach 4	68	0
21-Apr	Bay Creek & Stevens Reach 6	0	0
26-Apr	Gold Mine Creek and Stevens Reach 6	3	0
6-May	Unnamed Tributary and Stevens Reach 3	0	0

Breeding migrations.— In 2019, I observed a total of 954 *T. rivularis*, including four amplexing pairs and groups, across nine survey dates between 16 March 2019 and 12 May 2019 in both Stevens Creek Reach 4 and Twitty Creek (Table 2), although many individuals may have been captured more than once. I captured and measured 80 adult males, (mean SVL = 68.6 mm ± 0.5 mm; range, 55–76 mm) and eight juveniles (mean SVL = 28.0 mm ± 1.4 mm; range, 23–35 mm). All adult *T. rivularis* captured were confirmed to be males with the exception of three amplexing pairs and an amplexing group of three on 14 April 2019 in which sex was not assessed due to permit requirements. It is likely that at least one individual in an amplexing pair/group was a female.

In Stevens Creek Reach 4, observations of *T. rivularis* increased to a peak of 373 observed individuals on 24 March 2019 and fell to 92 observations four weeks later on 27

April 2019 (Table 2). *T. granulosa* and *T. torosa* numbers in Stevens Creek were lower

than *T. rivularis*, and peak encounter timing was later. *T. granulosa* detections increased

steadily from one observation on 16 March 2019 to 74 observations on 12 May 2019

(Table 2). I first observed three *T. torosa* individuals on 13 March 2019 and numbers

increased to 23 individuals on 27 April 2019 (Table 2).

Table 2. Count Data for Each Species Observed During Each Survey Date in 2019

Location	Date	*Taricha rivularis*	*Taricha torosa*	*Taricha granulosa*	*T. torosa/ granulosa*	*Dicamptodon ensatus*
Stevens Creek	16 Mar 19	84	0	1	0	0
	24 Mar 19	373	3	4	2	0
	14 Apr 19	343	6	49	6	0
	27 Apr 19	92	23	45	18	2
	12 May 19	0	18	74	10	1
Twitty Creek	17 Mar 19	13	1	8	22	2
	3 Apr 19	29	51	53	3	4
	23 Apr 19	17	48	103	13	21
	11 May 19	3	52	58	7	17

In the Twitty Creek surveys, *T. rivularis* numbers were much smaller than on Stevens

Creek (Table 2). The initial Twitty Creek observations peaked at 29 individual

observations (26 adult males and 3 juveniles) on 3 April 2019 and then decreased to 17

adult males on 23 April 2019 ending the season at three individuals (1 male and 2

juveniles) on 11 May 2019. *T. granulosa* and *T. torosa* observations, in contrast, were

more abundant in Twitty Creek compared to Stevens Creek (Table 2).

    Breeding aggregation.—Using observations from all dates sampled, the southern *T.*

rivularis population displayed clustered distributions in both Stevens (*NNR* = 0.22; *Z* = -

42.29, $P < 0.01$) and Twitty ($NNR = 0.45$; $Z = -7.95$; $P < 0.01$) Creeks, although the overall number of detections was smaller in Twitty.

The nearest neighbor analyses by sampling date for Stevens Creek in particular showed consistently clustered distributions throughout the season: on 24 March 2019, the NNR was 0.19 ($Z = -29.81$; $P < 0.01$), on 14 April 2019, the NNR was 0.24 ($Z = -27.03$; $P < 0.01$), and on 27 April 2019, the NNR was 0.40 ($Z = -11.05$; $P < 0.01$). In Twitty Creek, however, distributions initially alternated between randomly distributed across the landscape (17 March 2019: $NNR = 1.14$; $z = 0.95$; $P = 0.34$ and 24 April 2019: $NNR = 1.13$; $Z = 1.05$; $P = 0.29$) and clustered (3 April 2019: $NNR = 0.58$; $Z = -4.34$; $P < 0.01$), but remaining individuals were ultimately over-dispersed by the end of the season (11 May 2019: $NNR = 6.37$; $Z = 17.78$; $P < 0.01$) in Twitty Creek (Table 3).

Habitat use and availability.— Available habitat in Stevens Creek differed detectably from habitat in Twitty Creek ($\chi^2 = 29.87$, df $= 4$, $P < 0.001$). The first 223 m of the Stevens Creek reach consisted of cascades separated by runs and pools. The habitat upstream of the cascades was sinuous flat-water runs, separated by pools and riffles. The mean width of the aquatic habitat within the Stevens Creek reach was 3.6 m (1.52 m to 8.66 m). The most available mesohabitat within the Stevens Creek reach was run or flatwater (566 m; 56.7%). Pools comprised 167.2 m (16.7%) of available habitat, with a mean depth of 0.63 m (0.40 to 1.01 m). Riffles or turbulent water (144.1 m; 14.4%) were the next most abundant habitats available, followed by high gradient turbulent water or cascades (121.6 m; 12.2%).

Table 3. Average Nearest Neighbor Analysis.

	Twitty					Stevens			
	All Dates	17-Mar	3-Apr	24-Apr	11-May	All Dates	24-Mar	14-Apr	27-Apr
Observed Mean Distance	12.41	43.08	44.06	18.48	247.83	1.50	1.41	2.36	4.83
Expected Mean Distance	27.32	37.86	76.14	16.31	38.93	6.73	7.31	9.96	12.12
Nearest Neighbor Ratio	**0.45***	**1.14§**	**0.58***	**1.13§**	**6.37¥**	**0.22***	**0.19***	**0.24***	**0.40***
z-score	-7.95	0.95	-4.34	1.05	17.78	-42.29	-29.81	-27.03	-11.05
P	0.00*	0.34§	0.00*	0.29§	0.00¥	0.00*	0.00*	0.00*	0.00*

Note: § = Non-significant ($P > 0.05$); accept the null hypothesis; random distribution. * = Significant ($P < 0.05$) and NNR > 1.0, clustered distribution. ¥ = Significant ($P < 0.05$) and NNR < 1.0, dispersed distribution.

The aquatic habitat within Twitty Creek averaged 1.82 m in width, ranging from a minimum of 0.82 m to a maximum of 9.54 m. The most abundant mesohabitat was again run or flatwater (488.7 m; 56.5%), but in Twitty Creek, riffles or turbulent water were the next most abundant habitat available (208.9 m; 24.1%). Pools comprised 138.3 m or 16.0% of available habitat with a mean depth of 0.40 m and ranging from 0.67 m to 0.27 m in depth. High-gradient turbulent water or cascades were not present, but Twitty Creek also had a large (18.8 m) log jam present within the creek representing 2.2% of the available instream habitat.

In Stevens Creek, available habitat and habitat use by each *Taricha* newt differed significantly ($\chi^2 = 48.234$, df = 6, $P < 0.05$). Within Stevens Creek, flatwater runs were the most common mesohabitat used by *T. rivularis* (Table 4). Pools were the next most common mesohabitat used, followed by riffles. *T. granulosa* and *T. torosa*, in contrast, were most commonly observed in pools, followed by runs and riffles (Table 4).

Table 4. Count of Mesohabitat Use by Each Species Encountered

Location	Mesohabitat Type	*Taricha rivularis*	*Taricha torosa*	*Taricha granulosa*	*T. torosa/ granulosa*	*Dicamptodon ensatus*
Stevens	bank	47	2	10	0	0
	cascade	1	0	1	0	0
	pool	290	33	85	29	2
	riffle	164	0	12	0	0
	run	389	15	65	7	1
Twitty	bank	31	66	68	24	1
	pool	11	33	75	13	27
	riffle	6	5	6	0	1
	run	10	48	73	7	14

In Twitty Creek, I observed *T. rivularis* most commonly on the bank (31 individuals, 53.4%), not in-stream (Table 4). *T. granulosa* and *T. torosa* were observed in greater numbers in Twitty Creek compared to *T. rivularis*, but, similarly, in Twitty Creek, over a third of the observed *T. granulosa* and *T. torosa* were on the bank. For in-stream Twitty Creek habitat, *T. rivularis* was most commonly found in pools and runs, similar to *T. granulosa* and *T. torosa* (Table 4).

I found a total of six variables to be predictive of male *T. rivularis* and *T. granulosa* habitat use in the final selected model of the binary logistic regression. Both Riffle (ß = -1.86, SE 0.35, $P < 0.05$) and Run (ß = -0.61, SE 0.19, $P < 0.05$) mesohabitats were associated more with *T. rivularis* than Pool (Table 5). For nearest cover type, *T. rivularis* tended to be associated more with Water Depth compared to the reference category of Interstitial Spaces, but the relationship was statistically weak (ß = -0.60, SE 0.32, p < 0.06). *T. granulosa* was more strongly associated with Woody Debris (ß = 0.48, SE 0.24, $P = 0.04$) and Undercut (ß = 0.71, SE 0.22, $P < 0.05$) than with Interstitial Spaces. For substrate, *T. granulosa* was more strongly associated with Cobble (ß = 2.29, SE 1.05, $P = 0.03$) and Silt or Organic Matter (ß = 2.30, SE 0.1.05, $P = 0.03$) than with the reference category of Boulders (Table 5).

Table 5. Binary Logistic Regression Results for Habitat Use

	ß	SE	Z	P	OR	Confidence Interval 2.50%	97.50%
(Intercept)	-2.80	1.04	-2.70	**0.01***	0.06	0.00	0.30
Mesohabitat: riffle	-1.86	0.35	-5.33	**<0.05****	0.16	0.07	0.30
Mesohabitat: run	-0.61	0.19	-3.21	**<0.05****	0.54	0.37	0.79
Substrate: cobble	2.29	1.05	2.18	**0.03****	3.61	0.71	65.92
Substrate: gravel	1.28	1.04	1.23	0.22	9.88	1.89	182.43
Substrate: S/O	2.30	1.05	2.19	**0.03****	10.01	1.91	184.67
Substrate: sand	1.69	1.04	1.63	0.10	5.45	1.07	99.50
Cover: OM/veg	0.52	0.31	1.70	0.09	1.69	0.91	3.04
Cover: undercut	0.71	0.22	3.27	**<0.05****	2.04	1.33	3.14
Cover: water depth	-0.60	0.32	-1.87	**0.06***	0.55	0.28	1.00
Cover: woody debris	0.48	0.24	2.01	**0.04****	1.62	1.01	2.60

Note: Reference category for mesohabitat was pool. Reference category for substrate was boulder. Reference category for cover type was interstitial spaces. ß = coefficient; SE = Standard Error; Z = the Wald's Test statistic (standard deviations); OR = odds ratio or the exponent of ß. The (+) denotes a positive association with T. rivularis and (-) denotes negative association with *T. rivularis.*

Oviposition site selection.—I detected a total of 58 *T. rivularis* egg masses across 17 oviposition sites in Stevens Creek Reach 4 (Table 6). I observed 61% of oviposition sites in runs, 22% in riffles, and 17% in pools. The mean attached-substrate size was 1.52 m^3 (range, 0.22–11.68), and the attached substrates were either classified as a boulder (50%) or cobble (44%), with one oviposition site on a large piece of wood containing 13 egg masses. Ten of the 17 oviposition sites, representing 39 of the 58 egg masses (67%), were located in one 30 m section of Stevens Creek.

Table 6. Oviposition Site Characteristics and Measurements

	Mean	Min	Max
Number egg masses per oviposition site	3.41	1.00	13.00
Attached Substrate Size (m²)	1.52	0.22	11.68
Depth (m)	0.16	0.03	0.30
Distance from Bank (m)	1.12	0.24	2.44
Canopy Cover (%)	85.62	68.80	100.00

Binary logistic regression revealed that each unit increase of substrate size increased the probability of egg mass presence on a substrate by 40% ($ß = 2.68$, SE 1.33, $P = 0.04$; $W = 75$, $p = 0.017$) (Table 7, Figure 4).

Table 7. Binary Logistic Regression Results for Oviposition Site Selection.

|	ß	SE	z	p	Odds Ratio	Confidence Intervals 2.50%	97.50%
(Intercept)	-1.55	0.76	-2.04	0.04	0.21	0.04	0.82
Substrate Size (m³)	2.68	1.33	2.02	0.04	14.63	1.79	343.80
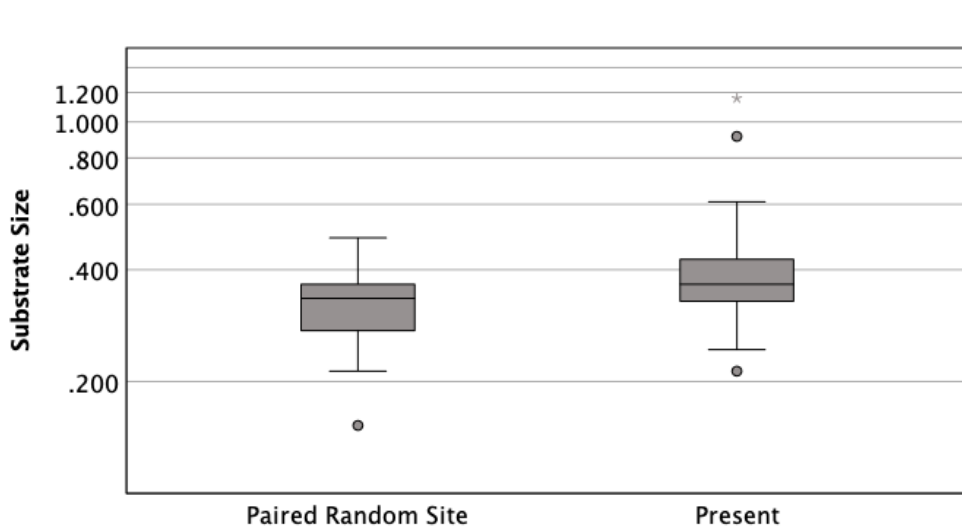
Figure 4. Oviposition site substrate size in comparison to paired random unoccupied sites on a log scale.

Range of southern population.—The southern population of *T. rivularis* was discovered in 2009 (Reilly et al. 2014) in the Upper Stevens Creek watershed, but until 2018, no surveys had been conducted in the surrounding watersheds to determine the extent of the range of this population. Based on our surveys from the winter and spring of 2018, the population aggregates in a 1000 m section of Stevens Creek and Twitty Creek. To the west of Stevens Creek and in the adjacent watersheds, surveys were conducted in Lambert Creek and its tributaries once. These surveys did not confirm the absence of *T. rivularis* in these streams. More surveys need to be conducted to confirm the presence or absence of *T. rivularis* in these adjacent watersheds and streams especially in areas of redwood forests where the species is generally found (Packer 1960; Reilly et al. 2014).

Surveys of the tributaries to the east of Stevens Creek were all short distances upstream due to the steep incline and heavy vegetation overgrowth. In addition, those streams all had calcified deposits on the stream channel with a lack of boulder and cobble substrate and any substantial flow which makes the tributaries to the east of Stevens Creek unsuitable for breeding *T. rivularis* (Twitty 1942; Twitty 1966). Other than Twitty Creek, one other tributary was surveyed to the west of Stevens Creek, the unnamed tributary 200 m south of the Twitty-Stevens confluence. I observed one *T. rivularis* individual on the bank on 16 April 2018. This observation was two days before Stevens Creek Reach 4 survey when *T. rivularis* individuals were already dispersing at the end of

the breeding season. The presence of just one individual on the bank of the creek during the out-migration suggests that this observation was of a dispersing individual.

Breeding movements.—The Pepperwood Creek experiments conducted by Victor Twitty and others in Sonoma County concluded that breeding adult *T. rivularis* individuals begin moving towards breeding locations in late January and arrive in the stream once the spring rains begin to subside (Packer 1960; Packer 1963; Twitty 1966; Twitty et al. 1966). The breeding pattern of the southern population suggests a similar breeding period that starts in mid-March and abruptly ends in late-April.

The 2019 breeding surveys described an obvious change in magnitude of breeding migration into and out of the creeks. Due to multiple storms in early March, surveys began on 16 March 2019 and a large number of males were already present in Stevens Creek Reach 4 during the initial survey. The following surveys and the obvious aggregation of breeding males in Stevens Creek followed by the abrupt end six weeks later provided a general migratory breeding pattern. During the 27 April 2019 survey, I observed many individuals still within the stream moving toward shore and attempting to climb up near-vertical banks. This behavior indicated that many individuals still present in the channel were finished breeding and dispersing upland.

This breeding migration pattern is similar to what was described in the Pepperwood Creek experiments; breeding began in March and abruptly ended mid-to-late-April. Males typically arrived a few weeks before the females and females were only present for a few days (Davis and Twitty 1964). In another population studied by Twitty, breeding

occurred in April, indicating some phenotypic plasticity in breeding patterns (Twitty 1942; Packer 1960; Twitty 1966; Petranka 2010).

This phenotypic plasticity in breeding patterns was also observed in the southern population. During the initial survey of Stevens Creek Reach 4 on 18 April 2018, I observed 68 *T. rivularis* individuals. The following year, around the same time on 14 April 2019, I observed 343 *T. rivularis* individuals just below its peak. It was not until 27 April 2019 that *T. rivularis* numbers were at mid-April 2018 numbers indicating that the breeding season ended about two weeks later in 2019 compared to 2018. The later end (or later start) to the 2019 breeding season could result from the heavy storms in early March. Packer (1960) found heavy rainfall heavily influenced and inhibited movement toward the stream in the Pepperwood Creek population. In addition, rainfall is also the primary influence on movement out of the water during the breeding season and at the end of the breeding season (Packer 1960).

Habitat partitioning.—In Mendocino County, where *T. rivularis, T. granulosa,* and *T. torosa* co-occur, many observations were made by Victor Twitty (1942) that *T. granulosa* and *T. rivularis* would enter streams at the same time. In Stevens Creek Reach 4, *T. rivularis* had entered the stream before and in a much greater magnitude than *T. granulosa*. Additionally, in Mendocino County, both *T. rivularis* and *T. granulosa* would breed in different stream microhabitats. *T. torosa,* on the other hand, was present in neighboring systems, but was not present in the same stream that *T. rivularis* and *T. granulosa* were breeding in (Twitty 1942). The exclusion of *T. torosa* by *T. granulosa* has been documented in other parts of its range (AmphibiaWeb. 2021. *Taricha granulosa.*

Available from https://amphibiaweb.org/species/4288 [Accessed 5 July 2021]). Based on the numbers of *T. granulosa* and *T. torosa* in Stevens Creek Reach 4, fewer *T. torosa* were in the stream than *T. granulosa*. I did not observe any amplexing pairs or groups or other breeding behaviors of either *T. granulosa* or *T. torosa* during the 2019 surveys. This suggests that surveys did not extend far enough into the breeding season, as both *T. granulosa* and *T. torosa* typically breed until June. However, in the San Francisco Bay Area, *T. torosa* have not been observed breeding after April, and *T.* granulosa breeding usually ends even earlier (David Wake, pers. comm.). Alternately, both *T. granulosa* and *T. torosa* may be just passing through Stevens Creek on their way to the multitude of ponds within the watershed or to slower segments of Steven Creek. Many of the ponds in the watershed are sag ponds formed between the active fault zones. Sag ponds are ideal for breeding for *T. torosa* and *T. granulosa,* with clear and deep water year-round.

Available habitat.—Both Twitty Creek and Stevens Creek are in the same watershed and are relatively similar in terms of mesohabitat availability. The biggest difference between the 2 streams is that Stevens Creek Reach 4 contains approximately 200 m of fast-flowing cascades while Twitty Creek does not. The dimensions of the stream, however, are much different. Stevens Creek Reach 4 is almost twice as wide as Twitty Creek which may affect breeding success as narrower streams have more erratic flows, especially during storms. Erratic flows could potentially cause larvae or egg masses to wash out or be destroyed if high-energy flows cause the movement of large rocks and

other material. With a broader channel, Stevens Creek has an area with flood plains

which provides more room for storm flows to spread out (Rosgen 1994).

The presence of complex habitat features of Stevens Creek most likely affected the

reproductive success of *T. rivularis* throughout the years. Complex habitat features are

known to be beneficial to many species, including but not limited to salmonids (Beechie

et al. 2005; Solazzi et al. 2011), frogs (Lind et al. 1996; Fellers and Kleeman 2007), and

invertebrate food sources (Gregory et al. 1991). I observed rainbow trout and multiple

invertebrate species during surveys.

Twitty Creek or Stevens Creek.—Surveys and analysis of the distribution of *T.*

rivularis in both Stevens Creek Reach 4 and Twitty Creek suggest that Stevens Creek

Reach 4 and not Twitty Creek is where *T. rivularis* are aggregating for breeding. The

presence of egg masses only in Stevens Creek suggests that the southern population of *T.*

rivularis is only breeding in Stevens Creek Reach 4. Finally, the presence of juveniles

only in Twitty Creek suggests that Twitty Creek may only be in the path of dispersing

juveniles after transformation (Twitty et al. 1967; Petranka 2010). I did not observe any

juvenile *T. rivularis* in Stevens Creek Reach 4. Additional surveys and monitoring of this

population are needed to confirm this assumption.

Adult male habitat use.—The general habitat of *T. rivularis* is simply described by

Victor Twitty (1955) as mountain brooks or clean and rocky streams with moderately fast

flows. The southern population of *T. rivularis* has a greater association with the faster-

flowing mesohabitats (riffle and run) of the stream when compared to pool habitats.

Additionally, *T. rivularis* was more associated with water depth cover types over the

interstitial spaces of boulders and rocks. *T. rivularis* may thus prefer to use riffle and run

habitat with near deep pools for cover.

Taricha granulosa and *T. torosa* general breeding habitat is described as ponds, lakes,

or slow-flowing water of streams (Petranka 2010). The *T. granulosa* and *T. torosa*

population co-existing with the southern population of *T. rivularis* exhibit similar habitat

preferences and are more likely to be found in habitats with silty substrate, generally

found in pools and near undercut and woody debris cover types that are often in areas

with slow-flowing water. In southern California, however, *T. torosa* uses rapidly flowing

streams for breeding, and egg masses have been observed in runs and riffles (Gamradt

and Kats 1997)

Female oviposition site selection.—For egg mass placement, or oviposition site

selection, females deposit egg masses on the bottoms of large rocks within fast flowing

waters (Davis and Twitty 1964; Twitty 1966). The majority (67%) of observed

oviposition sites and egg masses occurred in an area where high densities of adults were

observed. Even with a small sample size, large substrate is the only habitat parameter

that appears to influence the probability of a female *T. rivularis* choosing a site to deposit

her eggs. Other habitat parameters such as water speed, canopy cover, depth, and

distance from bank could also influence the decision of the female *T. rivularis;* however,

more data is needed to confirm this hypothesis.

The availability of large substrates in well-oxygenated water is considered necessary

for reproductive success of *T. rivularis* (Twitty 1942; Twitty 1966). These habitats can

be affected by multiple factors, including timber harvest (Riley et al., 2005; Welsh &

Ollivier, 1998), agriculture (Blann et al. 2009), and urbanization (Welsh and Ollivier 1998; Riley et al. 2005), which can increased sediment inputs into the stream (Gamradt and Kats 1997; Kerby and Kats 1998). Increased sediment inputs alter flow regimes and the habitat and food sources for breeding *T. rivularis*.

Management implications.—The Upper Stevens Creek watershed is a relatively well-protected swath of land surrounded by MROSD parks and properties. The only disturbance to the Stevens Creek channel is the few hiking and mountain biking creek crossings. Unfortunately, many of the northern populations are not well protected. Much of the northern populations' habitat is becoming urbanized with buildings and roads or affected by agricultural practices.

The timing of breeding migration of *T. rivularis* could have implications for managers during the breeding seasons. Depending on the location of migratory barriers such as highly trafficked roads and trails, specific management practices may need to be put in place. For example, Tilden Regional Park of East Bay Regional Parks District (EBRPD) implement road closures of roads in the path of migrating *T. granulosa* and *T. torosa* (EBRPD. 2019. Newt Migration Closes South Park Drive in Tilden Regional Park. Available from https://www.ebparks.org/civica/press/display.asp?_layout=11&Entry=540 [Accessed 5 July 2021]). Similarly, Peninsula Open Space Trust and MROSD are conducting a newt mortality and population study in Santa Clara County, where over 11,000 newt mortalities have been documented since 2017 (MROSD. 2020. Agenda Item 6. https://www.open space.org/sites/default/files/20200923_Agmt_Newt _MortalityPopulationStudyAlmaBridgeRd_R-20-104.pdf [Accessed 5 July 2021]).

***Threats to the southern population of* T. rivularis.**—The most recent threat to the southern population of *T. rivularis* was an event intensified by climate change. The CZU Lightning Complex fire of 2020 burned 86,509 acres in the Santa Cruz Mountains and was stopped at Pescadero Creek, approximately 10 km away from the Stevens Creek watershed. Additional surveys in these areas are still needed to assess whether the southern population of *T. rivularis* extends further west to evaluate the effects of the CZU fire on the adjacent watersheds and their inhabitants.

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