CHANGES IN DEMOGRAPHY, DISTRIBUTION, AND DIET IN GARTER SNAKES FOLLOWING ERADICATION OF A NON-NATIVE PREY SUBSIDY

By

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ABSTRACT

CHANGES IN DEMOGRAPHY, DISTRIBUTION, AND DIET IN GARTER SNAKES FOLLOWING ERADICATION OF A NON-NATIVE PREY SUBSIDY

Justin Alexander Demianew

Interactions between non-native and native consumers are often complex and cryptic. I shed light on relationships between non-native brook trout (*Salvelinus fontinalis*), native amphibians, their shared predator (aquatic garter snake; *Thamnophis atratus*) and a sympatric amphibian specialist (common garter snake; *T. sirtalis*) using a treatment-control removal experiment in a sub-alpine system of northern California. Eradication of non-native *S. fontinalis* resulted in an immediate decrease in *T. atratus* abundance and survival, whereas their abundance increased in concert with *T. sirtalis* in an adjacent control basin. Additionally, *T. atratus* body condition decreased substantially during this time, despite their increased use of lentic breeding ponds and increased predation on native amphibians, including the first documented predation on coastal tailed frog (*Ascaphus truei*). My findings corroborate and strengthen previous research suggesting *T. atratus* abundance, and the resulting hyperpredation experienced by native amphibians, is likely linked with the presence of salmonids stocked for recreational angling in historically fishless waters. Additionally, there appears to be some degree of negative association between the two sympatric species of garter snake, but my study was not designed to fully investigate this relationship and the evidence provided herein is merely correlative. These results not only demonstrate how a single introduced species can have drastic and unintended consequences in seemingly pristine wilderness settings, they also illustrate how restoration-based management via removal of a single non-native species can aid in reshaping native food webs.

ACKNOWLEDGEMENTS

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This study is just one small slice of a much larger project aimed at understanding the ecology of high elevation herpetofauna in the face of anthropogenic perturbations. My thesis would not have been possible if it were not for all of those individuals who have laid the foundation for this project; who have sacrificed their blood, sweat, and tears collecting data in the field; who have given their time writing grant proposals to fund continued research; who have helped with data entry or acted as a sound board for conversation. The individuals mentioned herein all provided help in one way or another, and to all of them I am greatly indebted.

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most of the fish eradication. I also owe a thank you to Anthony Desch. With little more than a simple sketch on paper, Anthony constructed the ovagram I used to count embryos of ranid frog egg masses, a side project I conducted in tandem with my thesis research. My lab mates Ryan Baumbusch, Emily Cate, Lindsey Gordon, Alyssa Marquez, Shannon Murphy, Katrina Smith, and Claire Nasr were eager to constructively critique my research and were always willing to discuss methods, statistics, or general ecological theory. Dr. Brian Crawford happily shared his Jolly-Seber model code with helpful commentary, which assisted in my understanding of implementing open mark-recapture models under a robust design framework. To him and to all of these individuals, I am much obliged. To those at CDFW who provided logistical, managerial, or other support: Bernard Aguilar, Andrew Jensen, Karen Miner, and Laura Patterson; thank you as well.

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INTRODUCTION

The ubiquity of non-native species across the globe has resulted in wide-scale changes to many natural systems (Lever 1994, Williamson 1996, Asner and Vitousek 2005, Clavero and García-Berthou 2005, Ehrenfeld 2011, Simberloff 2011). Given the extent of introductions, non-native species have long been considered the second leading cause of biodiversity loss on a global scale (Vitousek et al. 1997) and the number one threat to native species in the United States (Czech and Krausman 1997). While we have made great progress in understanding the effects non-native species have on communities (Ricciardi et al. 2013), identifying the mechanisms contributing to these effects is a difficult but necessary task, especially before managers implement restoration actions. Ironically, restorative management actions typically involve the removal of non-native species to promote native biodiversity, but the outcomes of such actions can sometimes have unexpected and even detrimental consequences to native systems (e.g., Collins et al. 2009). These unintended outcomes can result when the effects of non-native species are masked by other species, such as in cases of apparent competition (Holt 1977, Holt and Lawton 1994), or when interactions between two or more non-native species are facilitative (*sensu* invasional meltdown; Simberloff and Von Holle 1999).

Hyperpredation is an example of both apparent competition and invasional meltdown. It describes the process by which non-native prey species indirectly affect native prey species by mediating an increase in abundance of a typically non-native shared predator (Smith and Quin 1996, Courchamp et al. 1999, 2000). Arguably, one of the most well-known cases of hyperpredation occurred on the Channel Islands off the coast of California (Roemer et al. 2001, Roemer et al. 2002). Here, non-native feral pigs (*Sus scrofa*) mediated an increase in abundance of golden eagles (*Aquila chrysaetos*) by serving as a food subsidy, which then resulted in hyperpredation on and a decline in native island foxes (*Urocyon littoralis*). The heightened predation experienced by *U. littoralis* was then exacerbated after a management action successfully removed the eagle's prey subsidy (Collins et al. 2009). This phenomenon of hyperpredation is not unique to the Channel Islands, however. It has been described in a wide array of taxonomic groups in both terrestrial (Smith and Quin 1996, Russell 2011) and aquatic systems (Ricciardi et al. 2001, Adams et al. 2003).

In the western United States, non-native salmonids are a force majeure in restructuring amphibian assemblages (Petranka 1983, Bahls 1992), and correlative evidence suggests non-native trout may have catalyzed hyperpredation by garter snakes on a native ranid frog (Pope et al. 2008). Pope et al. (2008) hypothesized that the introduction of non-native trout into high mountain lakes for recreational angling facilitated an elevational range expansion and increase in abundance in the aquatic garter snake (*Thamnophis atratus*). The addition of an aquatic predator to the sub-alpine food web resulted in increased predation on native amphibians, including the imperiled Cascades frog (*Rana cascadae*), a rare and declining species endemic to the Pacific Northwest (Pope et al. 2014). In addition to preying on sensitive amphibians, *T. atratus* may be competing for prey with the native common garter snake (*T. sirtalis*), a smaller, less aggressive amphibian specialist frequently present at these high elevation sites (Pope et al. 2008). This may be the only example supporting the hypothesis that non-native trout can have an indirect effect on a herpetofauna assemblage by mediating invasion by a native species.

My thesis aimed to experimentally assess the extent of hyperpredation described in Pope et al. (2008) by observing the effects of a removal experiment. From 2014 through 2017, the California Department of Fish and Wildlife (CDFW) removed non-native brook trout (*Salvelinus fontinalis*) in Echo Lake Basin as part of a restoration project aimed at restoring essential perennial wetlands for native amphibian populations (Demianew and Garwood, in prep). Using CDFW's fish removal effort as a treatment, I examined changes in *T. atratus* abundance, apparent survival, recruitment, somatic growth rate, body condition, spatial distribution, and diet before and after non-native fish eradication. Simultaneously, I monitored *T. sirtalis* demography and space use in an effort to test how perturbations in the invaded food web resulting from a management action (fish removal) might affect a sympatric predator.

There are many possible community responses that could follow the eradication of non-native fish, each of which could result in subtle or dramatic shifts in local food web structure. However, there are two scenarios that seem most likely given the hypothesized interspecific interactions between these predators and their prey (Pope et al. 2008). These scenarios might not be mutually exclusive, but they both serve to provide contrasting outcomes following fish removal (Figure 1). In one scenario, removal of non-native fish may result in restoration of the native food web (Figure 1A). If non-native trout facilitated the elevational range expansion and an increase in abundance

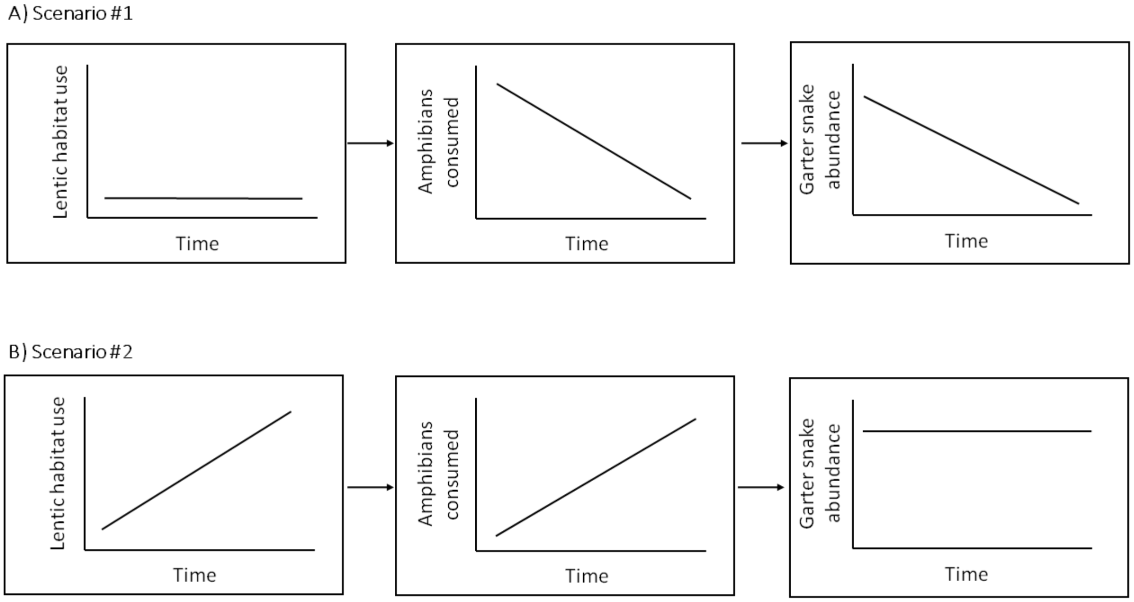

Figure 1. Examples of two possible outcomes that may result following the eradication of non-native trout. A) Scenario #1: *T. atratus* do not switch habitats from lotic to lentic, and either emigrate out of the basin or succumb to mortality. Here, fewer amphibians are consumed by garter snakes and the within-basin abundance of garter snakes decreases. B) Scenario #2: *T. atratus* switch from using lotic habitats to using lentic habitats; consequently, increasing their predation on native amphibians. Here, their within-basin abundance remains un-changed.

of *T. atratus*, then the removal of said trout may result in a decrease in *T. atratus* abundance via emigration out of the basin, reduced survival, reduced recruitment, or some combination thereof (Figure 1A). For example, if *T. atratus* is dependent on fish, it may be encouraged to leave the basin in pursuit of this limiting resource in other areas. In the absence of fish, *T. atratus* may experience reduced survival or recruitment driven by a reduction in body condition, which might translate to reduced somatic growth rates compared to areas with stocked fish populations. The overall reduction in *T. atratus* abundance might also lead to an overall decrease in the net predation on native amphibians by garter snakes (i.e., fewer snakes would eat fewer frogs), since approximately 40% of the diet of *T. atratus* consists of native amphibians in basins where *T. atratus* and trout co-occur (Garwood and Welsh 2007, Pope et al. 2008). Additionally, *T. atratus* may be competitively excluding *T. sirtalis* from wetland meadows where *T. atratus* occur at artificially high densities (Pope et al. 2008). If *T. atratus* abundance and distribution decrease following the eradication of trout, I might also expect to see an overall increase in the distribution of *T. sirtalis* within the treatment basin as they fill in habitats previously occupied by *T. atratus*.

Alternatively, *T. atratus* may persist following the removal of non-native fish (Figure 1B). Since *R. cascadae* comprises more than 40% of the total diet of *T. atratus* (Garwood and Welsh 2007, Pope et al. 2008), *T. atratus* may be able to persist at high abundances by prey switching following trout removal, increasing their overall net predation on native amphibians to make up for the loss of bigger, alternative fish prey. To maintain high abundances within the basin, however, *T. atratus* would likely be forced to expand its use of areas dominated by lotic (moving water) features where fish were eradicated into lentic (still water) habitats, which typically contain larval and metamorphic frogs (Garwood 2009), the preferred foraging habitat of *T. sirtalis* (Garwood and Welsh 2007, Pope et al. 2008). Following the postulate proposed in Pope et al. (2008), if indeed *T. atratus* competitively exclude *T. stirtalis*, then a range expansion in *T. atratus* within the treatment basin into peripheral amphibian breeding patches might result in a truncated spatial distribution in *T. sirtalis*.

Given the available evidence, each of the aforementioned scenarios are possible and the resulting dynamics might be a combination of both. In this vein, my thesis was exploratory in nature. Nonetheless, it emphasizes the importance and applicability of utilizing a management action (native species habitat restoration via removal of non-native trout) in an inductive experimental framework to test scientific hypotheses and provide additional insight into species' life histories (Oksanen 2001). Understanding how and why food web structures shift following a management action, even in seemingly simple systems, not only sheds light onto the complex nature of food webs, but it may also help inform management decisions and conservation plans aimed at restoring invaded ecosystems.

STUDY SPECIES

Aquatic Garter Snake (*Thamnophis atratus*)

The aquatic garter snake (family Colubridae) is currently split into three sub-species: the Oregon garter snake (*T. a. hydrophilus*), the Santa Cruz garter snake (*T. a. atratus*), and the Diablo Range garter snake (*T. a. zananthus*). Although *T. a. hydrophilus* is the sub-species present in my study area, I will refer to it as *T. atratus* for simplicity. *Thamnophis atratus* range from northwestern California into southwestern Oregon (St. John 2002) from sea level up to 2215 m (Garwood and Welsh 2010). Although rare, *T. atratus* have been observed in waterbodies 1,100 m above populations of salmonids (pers. obs.), but they appear to be most common at lower elevations in riverine habitats occupied by salmonids (Lind et al. 2005, Welsh et al. 2010). They are a medium-size garter snake generally ranging in length from 46 to 102 cm (Stebbins 2003), although populations in this high elevation study area are slightly smaller (21.4 cm total length for the smallest neonates to 87.8 cm for the largest adults, mean = 48.1 cm).

In the Klamath Mountains, *T. atratus* are often associated with fast-moving streams (Welsh et al. 2010), foraging diurnally on salmonids, including: Chinook salmon (*Oncorhynchus tshawytscha*), Coho salmon (*O. kisutch*), steelhead (*O. mykiss*), and coastal cutthroat trout (*O. clarkia clarkia*), as well as other aquatic vertebrates, such as coastal giant salamander (*Dicamptodon tenebrosus*) and foothill yellow-legged frog (*Rana boylii*) (Welsh and Lind 2000, Lind and Welsh 1994). At higher elevations, they regularly prey upon rainbow trout (*O. mykiss*), *S. fontinalis*, *R. cascadae*, Sierran treefrogs (*Pseudacris sierra*), and less frequently on Western toad (*Anaxyrus boreas*) (Garwood and Welsh 2007, Pope et al. 2008). In sub-alpine areas of the Trinity Alps Wilderness, neonate and juvenile *T. atratus* are especially prevalent in fish-free lentic habitats which support high concentrations of larval amphibians (Garwood and Welsh 2007, Pope et al. 2008). Despite occupying fish-free habitats, the overall distribution of *T. atratus* is closely tied to the presence of non-native salmonids, and correlative evidence suggests their high population densities in historically fishless areas are supported by non-native trout stocked for recreational angling (Pope et al. 2008).

Their success in a wide array of aquatic habitats is largely driven by several specialized feeding behaviors (Drummond 1983, Welsh and Lind 2000, Lind and Welsh 1994). These behaviors vary with ontogeny which allows small and large snakes to target and exploit different aquatic (Lind and Welsh 1994). For example, *T. atratus* have been observed utilizing a specialized tongue-flick from above the water's surface, referred to as lingual luring, to lure in aquatic prey (Welsh and Lind 2000). In the Klamath Mountains, *T. atratus* apparently mimic sticks or blades of grass (pers. obs.). Anchored by their tail to the substrate of the stream, they appear to undulate in the current as a stick or blade of grass would, typically within the bubble curtain of plunge pools or deep within mid-channel pools. The contrast of their dark scales and bright lateral stripe appears similar to vegetation, especially in dimly lit water. This technique likely allows for increased concealment for sit-and-wait predation. Additionally, unlike many species of garter snake, they can forage underwater for extended periods of time (>

20 minutes) in cold (< 10°C) headwater streams, and are successful at both ambush and sit-and-wait predation (pers. obs.).

Common Garter Snake (*Thamnophis sirtalis*)

The common garter snake (family Colubridae) is a widely-distributed snake in northern California and is one of the most successful reptiles in North America (Rossman et al. 1996), ranging from sea-level to 2450 m (Nussbaum et al. 1983). In California, *T. sirtalis* consists of 4 sub-species, and the valley garter snake (*T. s. fitchi*) is present in this study area (hereafter referred to as *T. sirtalis* for brevity). This species preys upon a myriad of vertebrates and invertebrates across its range; however, in the Klamath Mountains it is heavily associated with lentic amphibian breeding ponds where it feeds primarily on *R. cascadae* and *P. sierra*. Very occasionally, *T. sirtalis* also preys upon southern long-toed salamander (*Ambystoma macrodactylum sigillatum*), ensatina (*Ensatina eschscholtzii oregonensis*), rough-skinned newt (*Taricha granulosa*), and *A. boreas* (Garwood and Welsh 2007, Pope et al. 2008, Reilly et al. 2010). Similar to *T. atratus*, *T. sirtalis* is a medium size snake generally ranging in length from 46 to 140 cm (Stebbins 2003), but populations in this high elevation study area are slightly smaller (20.9 cm total length for the smallest neonates to 81.0 cm for the largest adults, mean = 45.9 cm). Although the impacts of non-native trout on native *T. sirtalis* in the Trinity Alps are unknown, non-native trout are thought to have resulted in the decline of native garter snakes in other regions of California by competing for their amphibian prey (Jennings et al. 1992, Matthews et al. 2002). The increase in *T. atratus* abundance mediated by non-native trout might potentially result in competitive exclusion of smaller *T. sirtalis* in areas within the Trinity Alps Wilderness (Pope et al. 2008).

Brook Trout (*Salvelinus fontinalis*)

Brook trout (family Salmonidae) are native to Eastern and Midwestern North America and range from Appalachia north to Maine and around the Great Lakes, but were introduced into high mountain lakes in the western United States (Bahls 1992), including the Klamath Mountains (Welsh et al. 2006), for recreational fishing. Today, they are a widely distributed species west of the Rocky Mountains (Fuller et al. 1999). In high mountain lake settings, they are generally self-sustaining, likely a result of their tolerance of frigid environments (Moyle 2002) and their ability to spawn in shallow lakes (Reimers 1958). Maturation of *S. fontinalis* is highly variable, ranging from 1 year (McFadden 1961) to 16 years (Reimers 1979). This plasticity likely facilitates establishment, persistence, and expansion of populations (Dunham et al. 2002). *Salvelinus fontinalis* have also been observed moving moderate distances of over 15 km (Adams et al. 2001) and up high gradient streams (Adams et al. 2000). Additionally, they are veracious predators with the ability to restructure native prey communities within one year of introduction (Reimers 1958). Given their predatory behavior, tolerance of cold water, prolific reproductive capabilities, and ability to disperse moderate distances over steep stream gradients, *S. fontinalis* introductions continue to have major impacts on native herpetofauna assemblages (Knapp and Matthews 2000, Knapp 2004, Vredenburg 2004, Knapp et al. 2007, Pope 2007).

STUDY AREA

This study was conducted in the upper reaches of the Deep Creek Watershed in Trinity County, CA (Figure 2). Specifically, field data were collected from two sub-basins in the southeastern portion of the Trinity Alps Wilderness, a 2,130 km^2 wilderness system within the Klamath Mountains of northern California. The northern-most basin, Siligo Basin, served as a control basin, and two meadow complexes were studied therein. These complexes were Lower Siligo Meadow (positive control – *S. fontinalis* were present and were not removed) and the South Siligo Meadow complex (negative control – currently and historically fishless). The southern-most basin, Echo Lake Basin, served as the treatment basin where *S. fontinalis* were removed over a period of four years (2014 - 2017). Within this basin, I focused my sampling on one meadow complex (Deep Creek Meadow), one lake (Echo Lake), a large ephemeral pond (Snowmelt Pond), and interconnected habitats. I also surveyed fishless habitats adjacent to my focal sites (e.g., Van Matre Meadow complex) to provide supplemental distribution data for garter snakes. Siligo and Echo Lake basins served as comparable study basins in that they are immediately proximate, have similar elevation (e.g., 6,435 m in Lower Siligo Meadow and 6462 m in Deep Creek Meadow), contain the same general suite of flora and fauna, they experience the same weather regimes, and have the same general aspect. The biggest difference between the two basins is Echo Lake Basin contains a small lake (1.1 hectares) whereas Siligo Basin does not (Figure 2). Despite this difference, most of the

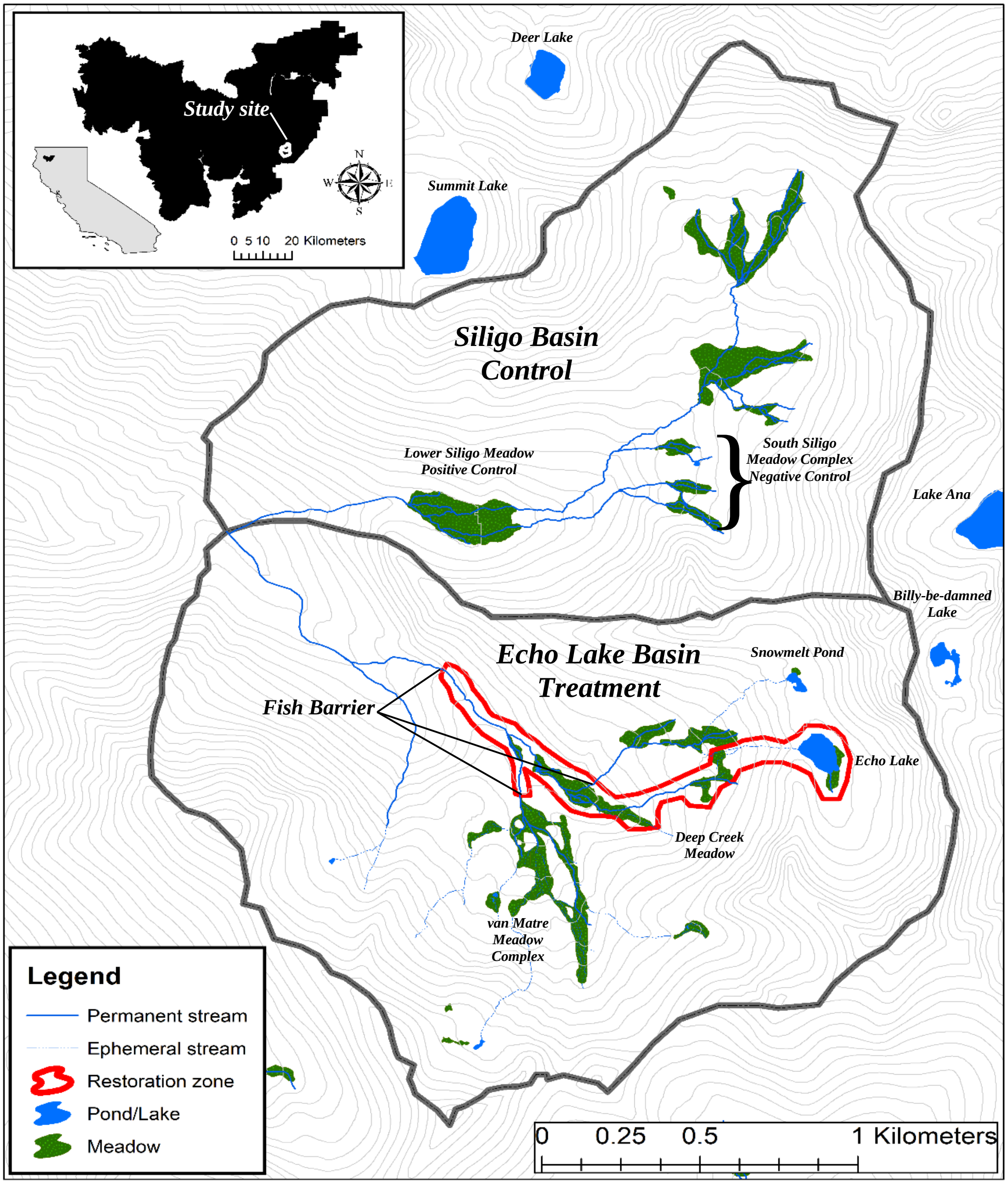

Figure 2. Control and treatment basins used to assess the impact of non-native fish removal on garter snakes. Siligo Basin consists of two control sites: Lower Siligo Meadow (positive control - fish present), and the South Siligo Meadow Complex (negative control – fish absent). Echo Lake Basin consists of two treatment sites: Echo Lake and Deep Creek Meadow, including adjacent and connected waters (e.g., Smowmelt Pond). Inset: Trinity Alps Wilderness, CA.

aquatic features and species of interest in this study were concentrated within the mosaic of wetlands common to each basin.

The vegetation of Echo Lake and Siligo basins is a mix of montane chaparral, open sub-alpine forest, and sub-alpine meadows with serpentine-tolerant plants. Forested areas are dominated by western white pine (*Pinus monticola*), foxtail pine (*P. balfouriana*), and Jeffrey pine (*P. jeffreyi*), whereas meadows contain sedges (Cyperaceae), grasses (Poacaeae), and a variety of flowering plants (Ferlatte 1974).

A Mediterranean climate typifies the Trinity Alps Wilderness and surrounding region. Precipitation usually falls as snow during the winter and early spring months (DWR 2018). Summers are typically warm and dry, but infrequent cold fronts resulting in precipitation (rain, hail, or snow) can occur (pers. obs.). Sheet flow from precipitation and snowmelt collects in a network of aquatic features, the majority of which are patchily distributed in meadow complexes (Garwood and Welsh 2007). These features are hydrologically connected during the late spring and early summer months when snowmelt is greatest. As the summer months progress, much of this ephemeral surface dries, causing greater isolation of remaining spring-fed perennial wetlands. For example, Echo Lake Basin alone experiences a 44% reduction in surface water area from spring to early winter (Garwood 2009). The remaining water features create a mosaic of habitats throughout the basin which function as an archipelago analog, although the degree of isolation between these island networks varies depending on the time of year and on the species of interest (Garwood and Welsh 2007).

Although the Trinity Alps Wilderness is protected under the Wilderness Act of 1964, it has been heavily impacted over the last 150 years from livestock grazing and through the introduction of a non-native trout fishery (Garwood and Welsh 2007). CDFW stocking records indicate that the first trout introduction occurred in 1930, when 10,000 *S. fontinalis* and 5,000 rainbow trout (*Oncorhynchus mykiss*) were planted in Echo Lake (Garwood and Welsh 2007). Stocking of Echo Lake sponsored by the California Department of Fish and Wildlife terminated in 1999, and an attempt was made to eradicate *S. fontinalis* from Echo Lake in fall 2003 (Pope 2007). However, trout removal was unsuccessful and a population of *S. fontinalis* persisted in Echo Lake and connected waters (i.e., Deep Creek) until 2016 when the CDFW eradicated the last observed *S. fontinalis* from the basin (Demianew and Garwood, in prep, Neely et al. 2018).

METHODS

CDFW implemented a restoration project in Echo Lake Basin from 2014 through 2017, removing 747 non-native *S. fontinalis* from one lake and approximately 1.6 km of stream habitat via gill nets, seines/block nets, electrofishing, while further minimizing reproduction by disturbance of redds (Demianew and Garwood, in prep) (Figure 2). All but a few *S. fontinalis* were removed prior to 2016, and those remaining were removed during summer 2016. Removal efforts continued through 2017 to insure complete basin-wide eradication. The focus of my research was assessing the response of herpetofauna to CDFW restoration activities, with a particular emphasis on garter snakes. As such, trout removal methods are not discussed in detail here, but are described at length elsewhere (Demianew and Garwood, in prep). All methods described hereafter focus on visual encounter surveys (VES) and capture-mark-recapture (CMR) for herpetofauna and the subsequent analytical techniques that were used to address my research objectives.

The following methods were approved by Humboldt State University's Institutional Animal Use and Care Committee (15.16.W.104-A). All activities were carried out under the direct supervision of a CDFW employee as part of CDFW's restoration project; consequently, a CDFW-issued Scientific Collecting Permit was not required.

Field Methods

Visual encounter surveys

I conducted VES to locate amphibians and reptiles following Garwood and Welsh (2007) based on procedures adapted from Crump and Scott (1994) and Thoms et al. (1997). Surveys were conducted from May through September 2016, May through October 2017, and April through October 2018 at each survey site between the hours of approximately 1000 and 1800, generally when sites were exposed to direct sunlight. I used a back-to-back robust sampling design (Pollock 1982), surveying each site for two consecutive days during each survey period, and each back-to-back survey was usually conducted every two weeks. I assumed closure (no births, deaths, immigration or emigration) between the successive days within each back-to-back sampling period. Surveys consisted of walking edges of all aquatic habitats, including ephemeral and permanent ponds, streams, and the interface between meadow complexes and adjacent upland areas in search of garter snakes. Streams greater than 1 m wide, ponds greater than 3 m wide, and Echo Lake were surveyed simultaneously by two or three crew members to increase detection probability and minimize the chance of losing animals after detection. Interstitial areas between water features within meadows were systematically searched using a zigzag approach similar to that described in Thoms et al. (1997). When meadow/stream-side vegetation obstructed the view of shorelines or narrow stream corridors, I used a dip net or hiking pole to part vegetation. Highly vegetated streams were always surveyed by two or more observers. I also surveyed wetland and upland habitats peripheral to my focal study sites to provide supplemental information on garter snake spatial distribution. Survey technique and sampling effort were consistent across each study site in 2016 and 2017. In 2018, there were no surveys conducted in July due to logistical constraints (fire/smoke and limited project funds). Lastly, pre-treatment data were available in Echo Lake Basin only, which was not surveyed using a back-to-back robust design during the pre-treatment years (2004-2006), but followed the same survey techniques.

Capture-mark-recapture

Marking and handling procedures are detailed in Garwood and Welsh (2007), and are summarized here. Once a snake was located during a VES, it was captured by hand or dip net, placed in a cotton bag, and its location noted using a handheld global positioning system (GPS) device. Each animal's weight was measured using a standard 30/60/100 g Pesola scale (Pesola®, Schindellegi, Switzerland) and a standardized snout-to-vent length (SVL) length (mm) was recorded. I standardized the length measurement by ensuring the animal was relaxed and fully elongated before recording its size, which is necessary to minimize sampling and observer variability, especially in larger snakes. Neonates, juveniles < 340 mm SVL, and gravid snakes were marked with a unique microbrand (Winne et al. 2006) or scale clip (Brown and Parker 1976). Non-gravid snakes ≥ 340 mm SVL were injected intra-coelomically with a passive integrated transponder (PIT) tag (8 mm x 1.35 mm FDX-B, Biomark Inc., Boise Idaho, USA). PIT tags were delivered using a sterilized single-use needle. Following application of marks, snakes were placed in their original cotton bag dampened with water. Once recovered, all animals were released at the site of capture. Handling time generally lasted between 2-5 minutes per animal. Anesthesia was unwarranted for these marking procedures.

Garter snake diet

To assess changes in garter snake predation on *S. fontinalis* and native sympatric amphibians, garter snakes were palpated to encourage regurgitation following Fitch (1987). Gravid female snakes were not palpated. Individual snakes recaptured with stomach contents were palpated again if: 1) a stomach sample was not obtained on the previous day's capture, or 2) more than two weeks elapsed since the last stomach sample was obtained. The number of prey, species, life stage, and weight were recorded for each stomach sample. After regurgitation, snakes were given the opportunity to re-consume their prey. Prey items not re-consumed were discarded at the site of capture.

Analytical Methods

CDFW and collaborating researchers have amassed a large historic dataset on the abundance and distribution of herpetofauna in the Trinity Alps Wilderness, including the basins used in this study. While most of the historic research has focused on *R. cascadae*, two years of CMR and distribution data (2004-2005) and three years of diet data (2004-2006) on garter snakes (*Thamnophis* spp.) were collected in Echo Lake Basin (Garwood and Welsh 2007). These data represent a snap-shot of garter snake natural history prior to basin-wide eradication of *S. fontinalis* and served to establish a pre-treatment baseline for garter snake demography, spatial distribution, and diet. Because fish were functionally extinct within the first month of the 2016 field season, 2016 through 2018 were considered post-treatment years for all analyses. Changes in this system as a result of non-native trout removal were made by comparing current trends to the historic data. Siligo Basin, however, has not undergone consistent long-term monitoring, and pre-treatment data does not exist for this site. Consequently, all analyses consider 3 treatment groups: 1) Pre-treatment - Echo Lake Basin (2004-2006), 2) Post-treatment - Echo Lake Basin (2016-2018), and 3) Control - Siligo Basin (2016-2018).

With the exception of the space-use analysis, all inferences were made in a Bayesian framework where the posterior probability distribution of model parameters was approximated using Markov chain Monte Carlo (MCMC). Bayesian inference has several advantages over typical frequentist approaches, including: 1) probabilistic statements can be made about the parameter(s) of interest, whereas probabilistic statements in frequentist statistics concern the data (which are real and observed) or the reliable of the method/estimator (e.g., 95% confidence interval); 2) hierarchical (e.g., mixed-effect) models are relatively easy to fit; 3) computing derived quantities with full propagation of error is straightforward without having to use more difficult approaches (e.g., delta method); 4) the estimates from Bayesian analyses are exact and do not rely on asymptotic assumptions in the maximum likelihood estimator, and 5) constructing models in a Bayesian framework fosters understanding of model structure since coded models appear similar to the written algebraic expression of the model (Kéry and Schaub 2012).

Unless otherwise noted, all statistical analyses were performed using the software JAGS version 4.2 (Plummer 2003) executed through R version 3.4.3 (R Development

Core Team 2017) using the R2jags package (Su and Yajima 2012). For all models implemented in the Bayesian framework, I examined model convergence using the Brooks-Gelman-Rubin convergence diagnostic (r-hat, Gelman and Rubin 1992, Brooks and Gelman 1997) and by visual inspection of trace plots. Goodness-of-fit was generally assessed using a posterior predictive check based on the Bayesian p-value. More parameters are reported as the mean ± 95% credible interval (95% CRI), unless otherwise noted. Last, rather than using indicator variables (Kuo and Mallick 1998) or some form of information criteria (e.g., WAIC) to rank a suite of candidate models to test *a priori* hypotheses regarding the potential responses of garter snakes to fish eradication, I elected to construct one 'full' model for each analysis consisting of variables of direct interest while accounting for confounding variables and base my assessment of 'effect' on the posterior distribution of the parameter(s) of interest (Kéry 2010).

Abundance, survival, and recruitment

To assess changes in abundance, survival, and recruitment in garter snakes following the eradication of *S. fontinalis*, I constructed a robust design hierarchical state-space Jolly-Seber model (Jolly 1965, Seber 1965, Appendix A). I collapsed each back-to-back survey effort into a single secondary occasion so that the resulting abundance estimates represented a single summer rather than a single survey. I only considered snakes larger than 330 mm SVL, which corresponds to animals in at least their third year of life (i.e., 2+) that have successfully recruited into the population as sub-adults or adults, the age at which many *Thamnophis* spp. begin to sexually mature (Carpenter 1952, Waye 1999, Rose et al. 2018). I restricted my analysis to these older age classes to avoid violation of the closure assumptions of this model by the pulse of neonates born mid to late summer. I fit the 'superpopulation' parameterization of the Jolly-Seber model (Crosbie and Manly 1985, Schwarz and Arnason 1996) following the model specification of Crawford et al. (2018) modified from Kéry and Schaub (2012). The model was fit using parameter expanded data augmentation (PX-DA; Tanner and Wong 1987, Royle et al. 2006, Royle et al. 2011), which consists of appending a large number of all zero encounter histories to the observed encounter histories. The augmented dataset includes the true population size (N), which is then analyzed using an indicator variable to describe whether or not an individual in the augmented encounter history is included in the population. A zero-inflated version of the original model is fit to the new augmented data set to account for the augmentation. PX-DA aids in computation by MCMC and allows greater flexibility in specifying individual effects. See Kéry and Schaub (2012) for an easy-to-follow description of data augmentation.

I estimated survival ($\widehat{\Phi}$) and conditional entry probability ($\hat{\eta}$) with group (species by basin) and year fixed effects. Conditional entry probability is the probability an animal enters the population in year *t*, given is has not yet entered in any previous year. I was not able to estimate site-level effects (e.g., positive control vs. negative control) due to relatively few captures of *T. atratus* in fishless sites and few captures of *T. sirtalis* in fish-occupied sites. I estimated availability ($\hat{\gamma}$) as a time-varying random effect specific to each group. Availability in this context is defined as the probability an animal is in the study area and available for sampling given it is alive at year *t*. I specified a basin-specific random effect of time on capture probability ($\hat{p}$), and allowed this to vary by species across each secondary occasion. I estimated per-capita recruitment ($\hat{f}$), abundance ($\widehat{N}$), and growth rate ($\widehat{\lambda}$) as derived parameters for each species by basin and year combination. I specified uninformative or weakly informative prior distributions for all parameters except survival, where I specified an informative prior from a beta distribution that reflects observed survival probabilities of *Thamnophis* spp. in the wild (Table 1). The beta distribution was used to limit estimation of unrealistic survival probabilities at or near one, which occurred in all model runs using uninformative priors [e.g., dunif(0,1)] and has been reported as an issue with this model type elsewhere (e.g., Halstead et al. 2011). The model was run on three chains with 300,000 iterations, a burn-in of 100,000 iterations, and each chain was thinned by 10. Consequently, inference for each parameter was made using a 60,000-iteration sample from the posterior probability distribution.

Somatic growth rate and body condition

To assess whether *T. atratus* are growing slower in the absence of introduced fish, I examined differences in their asymptotic growth rate between Echo Lake Basin and Siligo Basin from 2016 through 2018 using a von Bertalanffy growth model (Fabens 1965) modified from Eaton and Link (2011, Appendix B). The Eaton and Link (2011) parameterization of the von Bertalanffy model considers SVL as a latent (unobserved) state and accounts for measurement error and individual heterogeneity in growth and in the observed SVL using a non-decreasing gamma process (Eaton and Link 2011). I included a fixed sex effect on the gamma parameter (λ), which can be interpreted as the magnitude of individual heterogeneity in growth, with smaller values indicating more

Table 1. Prior distributions of parameters included in each analysis and statistical model.

Analysis	Model/ Parameterization	Parameter	Prior
Abundance, Survival, Recruitment	Robust design Jolly-Seber/ Superpopluation	Survival prob. ($\widehat{\Phi}$)	*Beta* (4,3)
		Conditional entry prob. ($\hat{\eta}$)	*Gamma* (1,1)
		Sd of availability ($\hat{\gamma}$)	*Uniform* (0,5)
		Sd of capture prob. ($\hat{p}$)	*Uniform* (0,5)
Somatic growth	von Bertalanffy/ Eaton and Link	Individual heterogeneity (λ)	*Uniform* (0,10)
		Sex effect on λ	*Uniform* (-1,1)
		Basin effect on λ	*Uniform* (-1.5,2)
		Asymptotic growth rate (k)	*Uniform* (0,5)
		Sex effect on k	*Uniform* (-2,6)
		Asymptotic length (L_∞)	*Uniform* (200,1000)
		Sex effect on L_∞	*Uniform* (-500,100)
Body condition	Gaussian glmm	Treatment intercept	*Normal (0, 0.001)*
		Treatment slope	*Normal (0, 0.001)*
		Sex effect	*Normal (0,1)*
		Sd of individual effect	*Uniform* (0,5)
		Residual sd	*Uniform* (0,100)
Microhabitat	Bernoulli glmm	Treatment intercept	*Normal* (0, *0.001)*
		Treatment*size slope	*Normal* (0, *0.001)*
		Sex effect	*Normal (0,1)*
		Sd of individual effect	*Uniform* (0,5)
Prob. of consuming native amphibians	Bernoulli glmm	Treatment intercept	*Normal (0, 0.001)*
		Treatment*size slope	*Normal (0, 0.001)*
		Sex effect	*Normal (0,1)*
		Sd of individual effect	*Uniform* (0,5)
# of native amphibians consumed	Poisson glmm	Treatment intercept	*Normal (0, 0.001)*
		Treatment*size slope	*Normal (0, 0.001)*
		Sex effect	*Normal (0,1)*
		Sd of individual effect	*Uniform* (0,5)

variation in growth. I also included a fixed sex effect on asymptotic length (L_∞) and fixed sex and basin effects on the asymptotic growth rate (k). The model was run using three chains with 300,000 iterations, a burn-in of 100,000 iterations, and each chain was thinned by 10. Inference for each parameter was made using a 60,000-iteration sample from the posterior probability distribution.

To investigate whether fish removal had an effect on *T. atratus* body condition, I used the length to weight ratio as an index of body condition before and after fish eradication. I considered all captures of known sex snakes ≥ 445 mm SVL. This size class was likely to be affected by the removal of a stream dwelling food subsidy since nearly 90% of snakes in this size range were observed foraging in streams, and the majority of historical diet samples obtained from snakes ≥ 445 mm SVL contained non-native fish. I constructed a generalized linear mixed effect model assessing the relationship between mass (response) and SVL across the three treatment groups. The model included interactive effects of treatment and SVL, a fixed effect of sex, and a random individual effect to incorporate the inherent correlation between mass and SVL over repeated captures of the same animal. I used uninformative or minimally informative priors for every parameter (Table 1). The model was run using three chains with 20,000 iterations, a burn-in of 5,000 iterations, and each chain was thinned by two. Inference for each parameter was made using a 22,500-iteration sample from the posterior probability distribution.

Home range and space use overlap

To assess changes in home range size and spatial distribution of garter snakes before and after trout eradication, I constructed and compared fixed-kernel utilization distributions (UDs). I constructed UDs in a maximum-likelihood framework because methods for UD analysis under the ML framework are better developed and more assessable than Bayesian methods. Utilization distributions are probabilistic home range models that estimate the intensity of use of a particular unit of space for a given animal (Van Winkle 1975). They are often used to estimate the area corresponding to a particular level of use (e.g, 50% core-use or 95% home-range area), to compare the joint probability of use or overlap between 2 animals (Millspaugh et al. 2004), or in resource selection studies (Millspaugh et al. 2006). I focus on these former two elements, but instead of describing space use for a particular animal, I constructed population-level UDs across both species of garter snake to assess how the size and overlap of their population-level home ranges change following eradication of a non-native fish. It is important to note these UDs only capture garter snake use of foraging habitat since surveys were not focused on garter snakes during rest, hibernation, or aestivation.

Construction of UDs involves selecting a bandwidth (smoothing) parameter that dictates the degree to which distant points determine the density estimate at any given point. Bandwidth selection is often the crux of constructing UDs (Gitzen et al. 2006). The two most common automatic bandwidth selection techniques in wildlife research include least squares cross validation (LSCV) and reference (Millspaugh et al. 2006). I constructed UDs using both of these techniques, but neither functioned well. The LSCV approach failed to converge for most UDs and the reference bandwidth selection method produced kernels that were unrealistic, resulting in predicted high-use areas coinciding with inhospitable foraging habitat (e.g., moraines or talus slopes). When habitat boundaries are sharp such as they are in my study area, kernel UD methods should be adapted (Millspaugh et al. 2006). Given this, I followed an approach similar to that described by Garwood (2009). I selected a bandwidth (h) parameter based on iteratively altering bandwidth values until the resulting UD for all locations across all years for both species of garter snake did not include large amounts of inhospitable foraging habitat outside of wetland patches. This global bandwidth value (h = 25) was then used for all subsequent UD subsets.

Traditional home range analyses generally focus on the individual as the sampling unit (Otis and White 1999) and population-level patterns are therefore inferred from the collection of individual home ranges (Fieberg and Kochanny 2005). However, this approach is not realistic in situations where individuals are too small to be radio-tracked, or when individual resight data are depauperate. In situations such as this, population-level processes of space use must be inferred from all detections of a particular species. Unfortunately, this approach makes it possible for marked individuals with frequent encounters to drive the perceived population-level spatial process. In order to alleviate the risk of single individuals with large encounter histories from over-influencing the UD of a particular species in a given area, and to eliminate spatial autocorrelation between captures of known individuals, some studies have included only one capture per individual per year (e.g., Pope et al. 2008). This approach, however, runs the risk of distorting the UD of a given species, especially if recaptures of individuals occur in sites other than their original capture. Moreover, excluding multiple captures may reduce the ability to assess the degree of activity in a site that is used consistently. For example, sites with an abundant food source might translate to greater levels of activity (i.e., frequent detections) compared to sites with poor food resources. Consistent and repeated detections of individuals at a particular site might indicate a site's importance to a particular animal or population carrying out aspects critical for growth and development, whereas single detections of animals away from these sites might be indicative of individuals dispersing or in search of alternative prey resources. Because I was interested in the total activity of each species, I included all locations of all individuals, in addition to locations of unknown individuals (e.g., identified to species but escaped before capture).

To assess changes in the area (ha) of space use before and after treatment, I calculated home range sizes based on fixed kernel UDs and estimated the percentage change in home range size in each species of garter snake between Echo Lake and Siligo basins from 2016 through 2018 and within Echo Lake Basin before and after treatment. Home range is a ubiquitous term in ecology that is individual-based and describes the area used to carry out normal activities such as food acquisition, mating, and raising progeny (Burt 1943). However, because I used animal locations pooled across individuals by species, home range is population-based in this context and is better thought of as the within-basin species range, but I will use the term home range herein for simplicity.

The degree of overlap in UDs between a pair of individuals or species can provide insights into individual or species interactions (Millspaugh et al. 2000). In experimental studies, when comparisons are made across years and between control and treatment sites, inference can be made about the degree to which a particular treatment may influence the observed space sharing. To assess the joint space use and degree of overlap between UDs from *T. atratus* and *T. sirtalis* before and after trout eradication, I estimated the following index of space use overlap:

volume of intersection (VOI)
$$\int_{-\infty}^{\infty}\int_{-\infty}^{\infty}\min[UD_1(x,y),UD_2(x,y)]\,dxdy \qquad (1)$$

where UD_1 and UD_2 are the utilization distributions of species 1 and 2, respectively. The VOI measures the shared volume between 2 animal's or population's UDs (Seidel 1992) and ranges from 0 to 1, indicating zero to complete overlap, respectively, between a particular pair of UDs.

Home range and overlap statistics were calculated for the 50% and 95% isopleth contours. I estimated the uncertainty in each metric by bootstrapping. Here, I created 10,000 bootstrap replicates (sampling with replacement) and constrained the size of each bootstrap dataset to be equal to that of the original dataset for each particular species by site by year combination. Utilization distribution, home range, and UD overlap statistics were estimated using the R package adehabitatHR (Calenge 2006). Sample sizes used to generate each statistic are included in Table 2.

Table 2. Number of locations used to construct fixed kernel utilization distributions for *T. atratus* and *T. sirtalis* in Echo Lake and Siligo basins, Trinity Alps Wilderness, CA.

Basin	Species	Year	# of locations
Echo	*T. atratus*	2004	69
		2005	27
		2016	57
		2017	17
		2018	26
	T. sirtalis	2004	78
		2005	19
		2016	29
		2017	54
		2018	22
Siligo	*T. atratus*	2016	86
		2017	123
		2018	134
	T. sirtalis	2016	21
		2017	34
		2018	19

Microhabitat use

Optimal foraging theory suggests altered resources should lead to habitat decoupling, wherein an individual or population shifts their habitat use to reflect the shift in available resources (Krebs et al. 1974, Charnov 1976). I used logistic regression to assess changes in the probability of *T. atratus* use of lentic habitats within Echo Lake Basin before and after trout removal and between Echo Lake and Siligo from 2016 through 2018. This was used to quantify the extent of movement from lotic (fish bearing) to lentic (amphibian rearing) habitats following the eradication of fish, and to assess the degree of similarity in *T. atratus* habitat use of lentic and lotic environments across populations of snakes from different basins.

I constructed a generalized linear mixed effect model with a Bernoulli response (1 = lentic, 0 = lotic) to estimate the probability of use in lentic vs. lotic waterbodies. I included a linear effect of SVL, which likely influences habitat use since size dictates prey availability (e.g., small snakes are gape limited) and prey types are distributed non-randomly across habitats (e.g., tadpoles are generally restricted to ponds). The model also included an interactive effect of treatment with SVL, and an individual random effect to model individual variation in use of a particular habitat. I used uninformative or weakly informative priors for all parameters (Table 1). The model was run using three chains with 50,000 iterations, a burn-in of 10,000 iterations, and each chain was thinned by five. Inference for each parameter was made using a 25,000-iteration sample from the posterior probability distribution.

Garter snake diet

To make up for the decrease in prey biomass resulting from fish eradication, it is plausible *T. atratus* would increase both the rate and number of native amphibians consumed. For example, a snake might have to consume 20 1.5 g tadpoles instead of one 30 g fish to make up for the reduction in energy per unit prey, and it could achieve this by feeding more frequently or ingesting more individual prey per feeding bout. To test the effect of fish eradication on *T. atratus* diet, I examined changes in the probability of palpating native amphibian prey from individual *T. atratus* in Echo Lake Basin prior to and after fish eradication. I also made comparisons between Echo Lake and Siligo basins in 2016 through 2018. I constructed a generalized linear mixed effect model with a Bernoulli response (1 = native amphibian, 0 = otherwise). I used uninformative or weakly informative priors for all parameters (Table 1). The model included interactive effects of treatment and SVL and a random individual effect. Each model was run using three chains with 100,000 iterations, a burn-in of 20,000 iterations, and each chain was thinned by 10. Inference for each parameter was made using a 24,000-iteration sample from the posterior probability distribution.

I compared the mean number of native amphibians palpated from individual *T. atratus* in Echo Lake and Siligo basins using a Poisson generalized linear mixed effect model. Because I was focused on possible changes in the number of native amphibians consumed per feeding bout, I only included snakes with native prey remains in their stomach sample (e.g., stomach samples with no prey or stomachs with non-native fish were excluded). This Poisson model mirrored the model structure and posterior probability distribution constraints from the Bernoulli glmm, above.

I was unable insure the availability of native amphibians was not different between pre- and post-treatment sampling periods since pre-treatment counts of larvae, metamorph, and small young-of-the-previous-year amphibians were not obtained prior to *S. fontinalis* removal. An alternative index to actual counts is the number of *R. cascadae* egg masses laid during pre-and post-treatment years. *R. cascadae* is the most abundant amphibian in the study area, and counts of their egg masses might be the only other index related to the relative numbers of larval and metamorphic amphibians, which are the life stages most common in the guts of *T. atratus* in this system (Garwood and Welsh 2007, Pope et al. 2008). The average number of egg masses encountered in Echo Lake Basin from 2004 through 2006 was 48, whereas the average number of egg masses laid in 2016 through 2018 was 57 (J. Garwood, unpub. data). This difference of nine egg masses is likely not biologically significant from a prey availability standpoint, however, since it would only take a few egg masses to produce enough larval and metamorphic amphibians in this basin to outnumber their garter snake predators by several orders of magnitude (e.g., an average *R. cascadae* egg mass contains approximately 375 embryos).

RESULTS

Demography

Abundance, survival, and recruitment

From 2016 through 2018 I captured 29 and 106 individual sub-adult and adult *T. atratus* in Echo Lake and Siligo basins, respectively. Over the same time period I captured 19 and 23 individual sub-adult and adult *T. sirtalis* in Echo Lake and Siligo basins, respectively. The number of captures per individual *T. atratus* ranged from one to four, and individuals were caught an average of 1.50 times each. The mean capture probability over this time period was estimated at 0.12 (95% CRI = 0.064 to 0.19) in Echo Lake Basin and 0.07 (95% CRI = 0.04 to 0.10) in Siligo Basin. This contrasts with pre-treatment (2004 to 2005) captures of individual *T. atratus*, which ranged from one to six captures per individual, and individuals were captured an average of 1.63 times each (capture probability: 0.09, 95% CRI = 0.05 to 0.14). The number of captures per individual *T. sirtalis* ranged from one to four in both the pre-treatment post-treatment years, and individuals were caught an average of 1.43 and 1.45 times, respectively, before and after non-native trout eradication. The mean capture probability in *T. sirtalis* was estimated at 0.06 (95% CRI = 0.03 to 0.10) in Echo Lake Basin prior to fish removal, 0.08 (95% CRI = 0.04 to 0.14) in Echo Lake Basin after fish removal, and 0.05 (95% CRI = 0.02 to 0.09) in Siligo Basin. No individuals of either species were captured in both the pre- and post-treatment sampling periods.

The abundance of both species decreased in parallel from 2004 to 2005. *Thamnophis atratus* decreased from 54 (95% CRI = 34 to 95) to 46 (95% CRI = 19 to 92) while *T. sirtalis* decreased from 65 (95% CRI = 44 to 99) to 45 (95% CRI = 21 to 84, Figure 3). From 2016 to 2018, *T. atratus* abundance decreased from 37 (95% CRI = 21 to 62) to 29 (95% CRI: 17 to 49) in Echo Lake Basin, partly driven by the incidental mortality of five animals in 2016 caused by fish eradication techniques. Their abundance increased over the same time period in Siligo Basin from 115 (95% CRI = 68 to 200) to 159 (95% CRI = 68 to 228; Figure 3). This translates to an overall post-treatment population

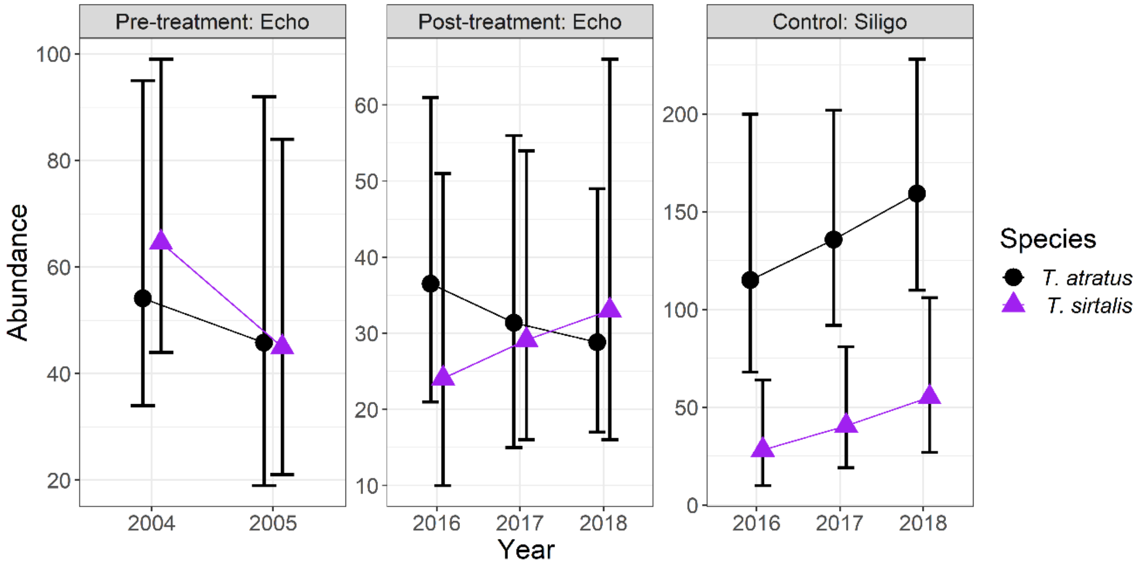

Figure 3. Derived abundance estimates and 95% CRIs for *T. atratus* and *T. sirtalis* in Echo Lake and Siligo basins from 2004 to 2005 and from 2016 to 2018, Trinity Alps Wilderness, CA. Model type: robust-design Jolly-Seber.

growth rate of 0.84 (95% CRI = 0.40 to 1.62) in Echo Lake Basin and 1.48 (95% CRI = 0.75 to 2.43) in Siligo Basin. There was a 0.90 probability that the 2016 to 2018 growth rate in the control basin was larger than that in the treatment basin over the same period ($Posterior_{\text{Siligo}} – Posterior_{\text{Echo}}$). In contrast, *T. sirtalis* abundance increased in both basins over this time, from 24 (95% CRI = 10 to 51) to 33 (95% CRI = 16 to 66) in Echo Lake Basin and from 28 (95% CRI = 10 to 64) to 55 (95% CRI = 27 to 106) in Siligo Basin (Figure 3), corresponding to an overall growth rate of 1.60 (95% CRI = 0.54 to 4.00) and 2.32 (95% CRI = 0.77 to 5.44) in Echo Lake and Siligo basins, respectively. Here, there was a 0.70 probability the overall growth rate in the control basin was higher than in the treatment basin over the same time period. Annual population growth rates for both species are shown in Figure 4.

Across both pre-and post-treatment sampling periods, apparent survival in *T. atratus* was lowest immediately following the eradication of non-native trout (0.52; 95% CRI = 0.24 to 0.83) and highest in the control basin from 2017 to 2018 (0.71; 95% CRI = 0.46 to 0.91; Figure 4). On the contrary, *T. sirtalis* apparent survival was highest in Echo Lake Basin from 2016 to 2017 (0.69; 95% CRI = 0.41 to 0.92) and lowest in Siligo basin from 2017 to 2018 (0.60; 95% CRI = 0.26 to 0.89), although the survival probability in *T. sirtalis* did not vary substantially across both basins (Figure 4).

Prior to fish eradication, per capita recruitment in *T. atratus* and *T. sirtalis* in Echo Lake Basin (2005) was estimated at 0.35 (95% CRI = 0.00 to 1.26) and 0.13 (95% CRI = 0.00 to 0.54), respectively (Table 3). These were among the lowest per-capita recruitment rates observed across all years. The highest per-capita recruitment rates were

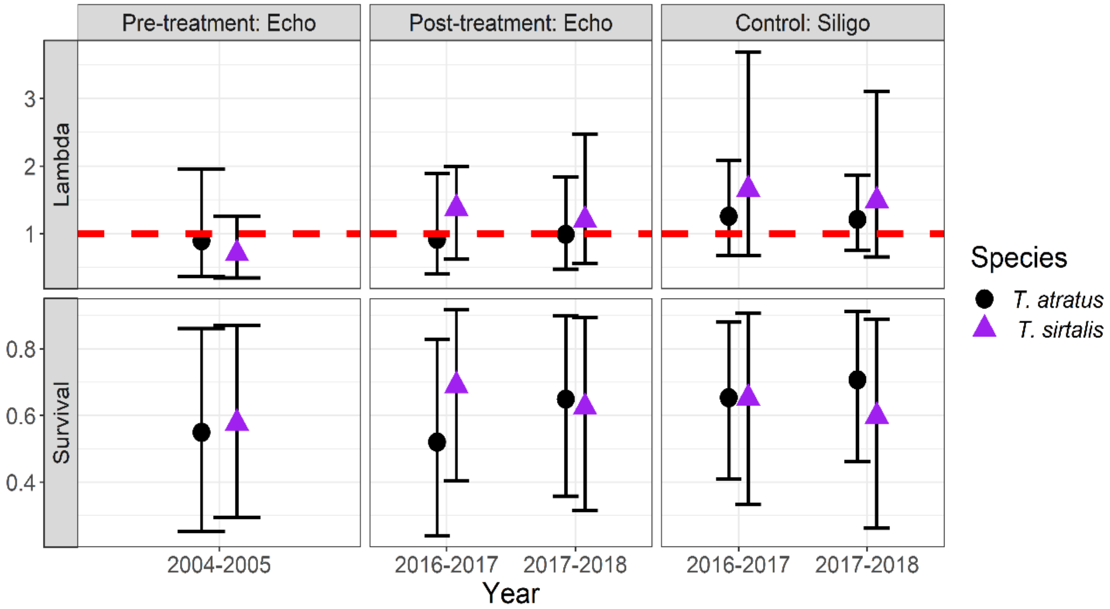

Figure 4. Population growth rate and survival probability (± 95% CRI) in *T. atratus* and *T. sirtalis* from 2004 to 2005 and from 2016 to 2018 in Echo Lake and Siligo basins, Trinity Alps Wilderness, CA. Values above the red dashed line (λ =1) indicate positive population growth whereas values below the line indicate negative population growth. Model type: robust-design Jolly-Seber.

Table 3. Per-capita recruitment estimates in *T. atratus* and *T. sirtalis* in 2005, 2017 and 2018 in Echo Lake and Siligo Basins, Trinity Alps Wilderness, CA. Model type: robust-design Jolly-Seber.

Basin	Species	Year	Estimate (95% CRI)
Echo	*T. atratus*	2005	0.347 (0.0-1.26)
		2017	0.406 (0.0-1.32)
		2018	0.319 (0.0-1.1)
	T. sirtalis	2005	0.127 (0.0-0.54)
		2017	0.642 (0.0-2.21)
		2018	0.56 (0.02-1.79)
Siligo	*T. atratus*	2017	0.60 (0.04-1.40)
		2018	0.50 (0.06-1.10)
	T. sirtalis	2017	0.98 (0.03-3.0)
		2018	0.56 (0.02-1.77)

observed in *T. sirtalis* in 2017 (Echo Lake Basin: 0.64, 95% CRI = 0.00 to 2.21; Siligo Basin: 0.98, 95% CRI = 0.03 to 3.00). *Thamnophis atratus* per-capita recruitment was lower on average, but generally followed the same trend as *T. sirtalis* from 2017 and 2018, decreasing slightly over this period (Table 3).

Somatic growth rate and body condition

I measured 264 growth increments from 99 individual *T. atratus* from 2016 through 2018. Overall, the predicted asymptotic length (L_∞) for female and male *T. atratus* was 709 mm SVL (95% CRI = 622 to 844) and 495 mm SVL (95% CRI = 454 to 540), respectively. The two sexes grew at substantially different rates. The asymptotic growth rate (k) in females was estimated at 0.48 (95% CRI = 0.31 to 0.54), whereas males grew nearly 1.49 times as fast (95% CRI = 0.37 to 1.92). The asymptotic growth rate in Siligo Basin was slightly smaller than in Echo Lake Basin (mean difference = -0.02; 95% CRI = -0.16 to 0.10). The average variation in individual female and male growth rates (λ) was approximately 0.91 (95% CRI = 0.13 to 5.01) and 0.71 (95% CRI = 0.08 to 4.48), respectively, with males displaying more variation in growth indicated by a smaller lambda.

I assessed differences in *T. atratus* body condition using 144 mass and length measurements on 89 non-gravid known-sex individuals ≥ 445 mm SVL. Overall, the weight to length ratio was slightly smaller in males, although this effect was miniscule (mean difference = -0.03; 95% CRI = -1.88 to 1.83). On average, post-treatment *T. atratus* were 10.30 g lighter (95% CRI = 2.78 to 17.80) than they were prior to fish eradication, and 6.28 g lighter (95% CRI = 0.67 to 13.17) than snakes of comparable size in Siligo Basin (Figure 5). However, the difference in the weight to length ratio was most obvious in large females (e.g., 600 mm SVL or +1 sd). At this length, the expected difference in weight between pre- and post-treatment Echo Lake Basin snakes was 23.5 g (95% CRI = 14.37 to 32.35).

Distribution

Garter snakes were typically encountered in amphibian breeding patches in both Echo Lake and Siligo basins or within fish bearing streams of Siligo Basin. With the exception of adult *T. atratus*, they were almost always detected in waterbodies containing larval, metamorphic, or juvenile/adult frogs. Adult *T. atratus* were usually encountered in streams where amphibians were undetected entirely or rarely seen, and in many cases (e.g., > 80% in Siligo Basin), adult *T. atratus* were encountered while actively foraging for fish.

Overall, the majority of garter snakes of both species were relatively site-faithful, with only five and 15 observations of individual *T. atratus* and *T. sirtalis* observed moving between sites in Echo Lake Basin and seven and one observations of individual *T. atratus* and *T. sirtalis* moving between sites in Siligo Basin. The greatest number of habitat patches an individual garter snake was captured in was three, and in the majority of cases movements between sites were unidirectional. Round-trip movements between sites were only observed in *T. sirtalis* in pre-treatment years. *Thamnophis atratus* was the only species observed moving between basins, with two individuals moving from Echo Lake Basin to Siligo Basin after fish eradication.

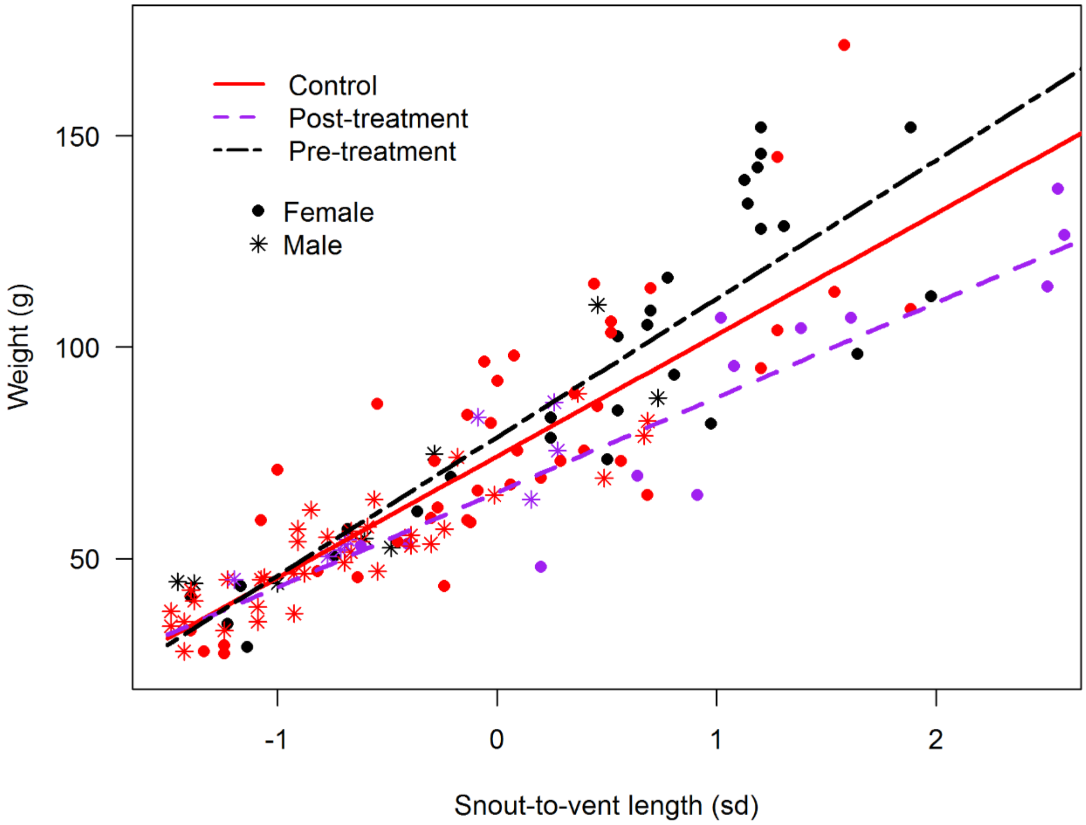

Figure 5. Predicted (dashed lines) and observed (points) relationship between the scaled snout-to-vent length (0 = an average size snake ≥ 445 mm SVL) and weight in male and female *T. atratus* in Echo Lake and Siligo basins, Trinity Alps Wilderness, CA. The difference in predicted weights are greatest between snakes in Echo Lake Basin prior to fish eradication and those in Echo Lake Basin following fish removal, but only in the largest animals.

Home range

Prior to the removal of *S. fontinalis* in Echo Lake Basin, the home range of *T. atratus* was approximately 0.59 (± 0.17 sd) and 6.93 (± 0.85 sd) ha at the 50% and 95% isopleths. Approximately 72% of the detections during this period occurred in Deep Creek Meadow, where *S. fontinalis* were abundant (Garwood and Welsh 2007). In 2016 through 2018, the mean home range of *T. atratus* increased 1.51 and 1.85 times at the 50% and 95% isopleths, respectively, but the core distribution did not shift from Deep Creek Meadow. This apparent within-basin range expansion during post-treatment years was largely driven by their 2016 distribution, where *T. atratus* were observed in many *R. cascadae* breeding patches outside of Deep Creek Meadow. However, this diffused distribution was highly ephemeral. By 2017, their distribution shrunk considerably by 67% and 69% at the 50% and 95% isopleths, respectively. In Siligo Basin their home range remained relatively constant year to year (Figure 6).

Overall, the home range of *T. sirtalis* shrunk considerably between pre- and post-treatment years, corresponding to their overall decrease in abundance between these sampling periods. In 2016 their home range size was nearly identical in size to *T. atratus* at the 95% isopleth, although their core use area was smaller (Figure 6). They then experienced a dramatic increase in their home range size from 2016 to 2017, in concert with their increase in abundance and the decline in home range area of *T. atratus*. Over the same period in Siligo Basin, the home range size of *T. sirtalis* varied little at both isopleths, similar to that observed in *T. atratus* (Figure 6).

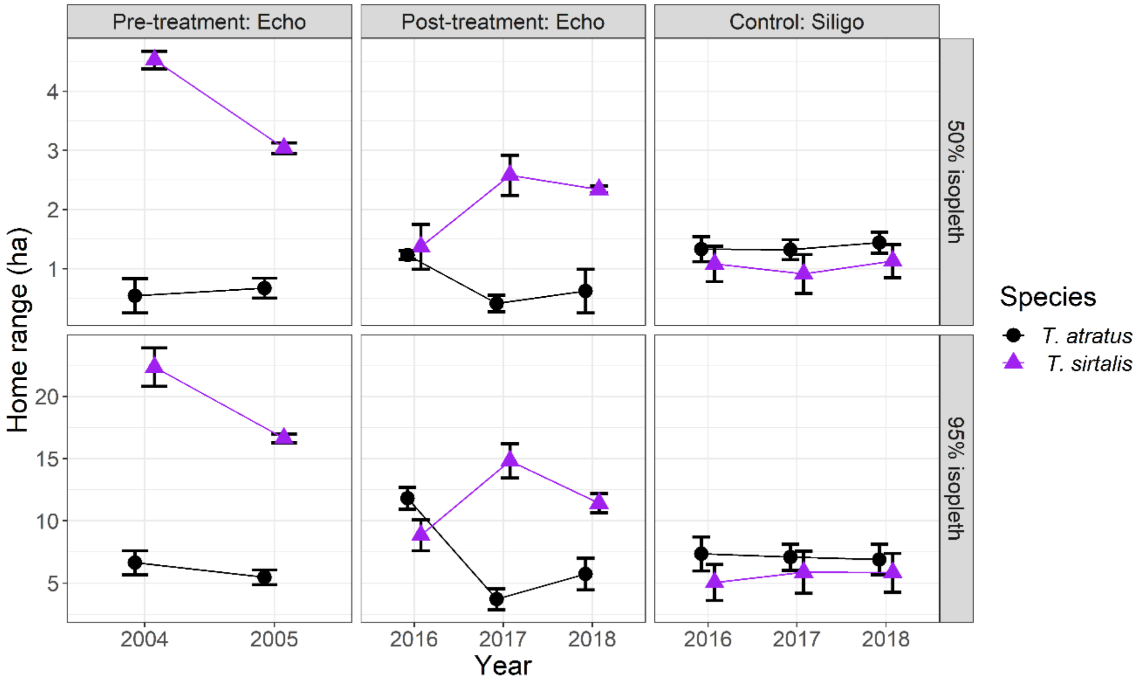

Figure 6. Home range size (± 1 sd) from fixed kernel utilization distributions in *T. atratus* and *T. sirtalis* in Echo Lake and Siligo basins from 2004 to 2005 and from 2016 to 2018, Trinity Alps Wilderness, CA.

Space use overlap

Overall, the distribution of *T. atratus* was more stable year to year compared to *T. sirtalis*, indicated by consistently higher values of space use overlap (Figure 7). *Thamnophis atratus* space use overlap in Echo Lake Basin between pre- and post-treatment years was 0.75 (± 0.10 sd) and 0.67 (± 0.06 sd) at the 50% and 95% isopleths, respectively. Considering only 2016 through 2018, space use overlap was much lower in Echo Lake Basin compared to Siligo Basin at both the 50% and 95% isopleths (Figure 7). In *T. sirtalis*, space use overlap in Echo Lake Basin between pre- and post-treatment years ranged from 0.29 (± 0.12 sd) and 0.38 (± 0.08 sd) at the 50% and 95% isopleths,

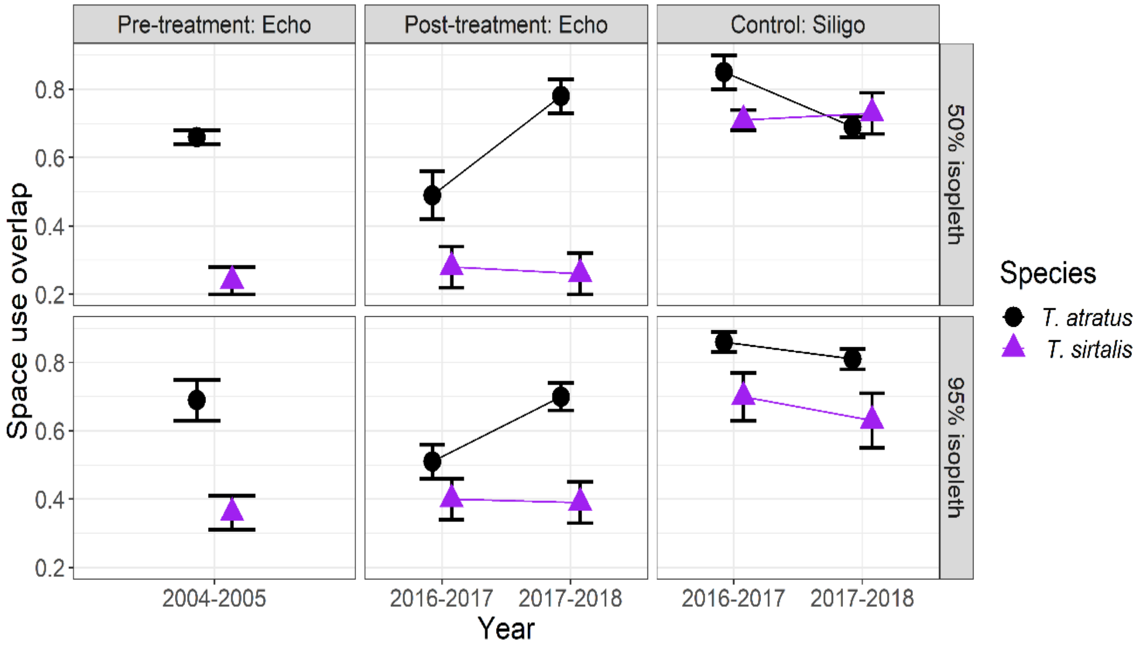

Figure 7. Volume of intersection/space use overlap (± 1 sd) between years within *T. atratus* and *T. sirtalis* at the 50% and 95% isopleths, Echo Lake and Siligo basins, Trinity Alps Wilderness, CA.

respectively. Similar to *T. atratus*, space use was more variable in the Echo Lake Basin compared to Siligo Basin from 2016 through 2018 (Figure 7).

In Echo Lake Basin, space use overlap between *T. atratus* and *T. sirtalis* ranged from 0.00 (± 0.01 sd) to 0.12 (± 0.05 sd) prior to fish eradication. From 2016 through 2018, their space use overlap increased steadily from 0.0 (± 0.05 sd) in 2016 to 0.17 (± 0.04 sd) in 2018 at the 50% isopleth. Their space use overlap was nearly identical at the 95% isopleths, with the exception of 2018, where their space use overlap was estimated at 0.28 (± 0.04 sd, Figure 8). In Siligo Basin over the same time period, space use

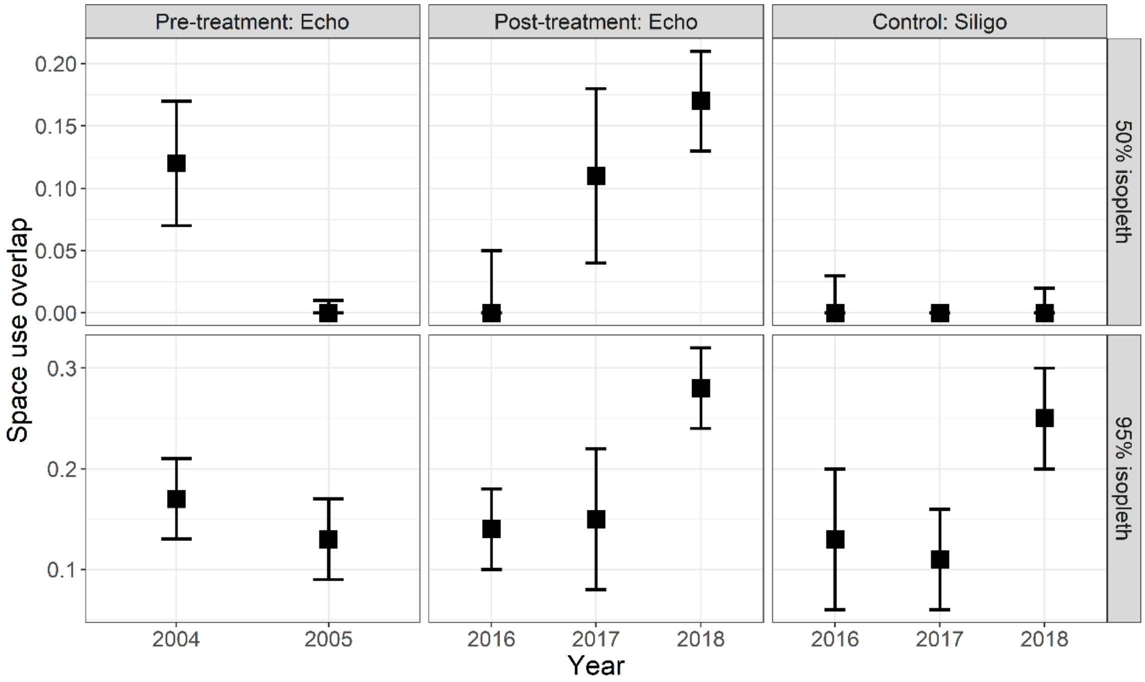

Figure 8. Volume of intersection/space use overlap (± 1 sd) between *T. atratus* and *T. sirtalis* at the 50% and 95% isopleths, Echo Lake and Siligo basins, Trinity Alps Wilderness, CA.

overlap between the two species was less than 0.05 at the 50% isopleth. With the exception of 2018, space sharing by *T. atratus* and *T. sirtalis* was generally less than 0.20 at the 95% isopleth (Figure 8).

Microhabitat use

In Echo Lake Basin from 2004 to 2006, *T. atratus* were detected in lotic features roughly 72% (81/112) of the time. During this period, the majority of lotic waterbodies occupied by *T. atratus* contained non-native *S. fontinalis* (Garwood and Welsh 2007, Pope et al. 2008). Within the first three years following eradication of *S. fontinalis*, the proportion of *T. atratus* captures in lotic water features decreased to approximately

33.7% (33/98). The predicted probability of detecting an average size (380 mm SVL) *T. atratus* in lentic habitats increased approximately 3 times from 0.23 (95% CRI = 0.12 to 0.37) to 0.71 (95% CRI = 0.53 to 0.87) during and immediately following the removal of non-native *S. fontinalis* (Figure 9). Over the same period, the probability of lentic habitat use by an average size snake in Siligo Basin was only 0.53 (95% CRI = 0.40 to 0.66). However, in large snakes (~600 mm SVL or +1.5 sd) the predicted probability of lentic habitat use in all treatment groups was less than 0.10.

Garter Snake Diet

Across all treatments, 601 prey items were palpated from 270 stomachs. Approximately 43 percent (n = 259) of all prey items were palpated from 78 stomachs prior to fish removal (2004 - 2006), while 342 prey items were palpated from 192 stomachs from 2016 through 2018. Although the number of prey items per snake varied greatly (1 to 33), the majority of snakes with prey contained only 1 prey item (Figure 10). Amphibians dominated the diets of both snake species compared to non-native fish, with larger snakes generally consuming larger prey (Figure 11).

In pre-treatment Echo Lake Basin, 18 of the 39 (46.2%) *T. atratus* with identifiable stomach contents contained native amphibians, totaling 97 individual native prey items. The remaining stomach samples with prey contained non-native *S. fontinalis*. In 2016 through 2018, 28 of 31 (90.3%) *T. atratus* consumed native amphibians, totaling 43 native prey items. The three *T. atratus* that did not consume native amphibians in 2016 through 2018 had consumed non-native trout in early 2016 when the

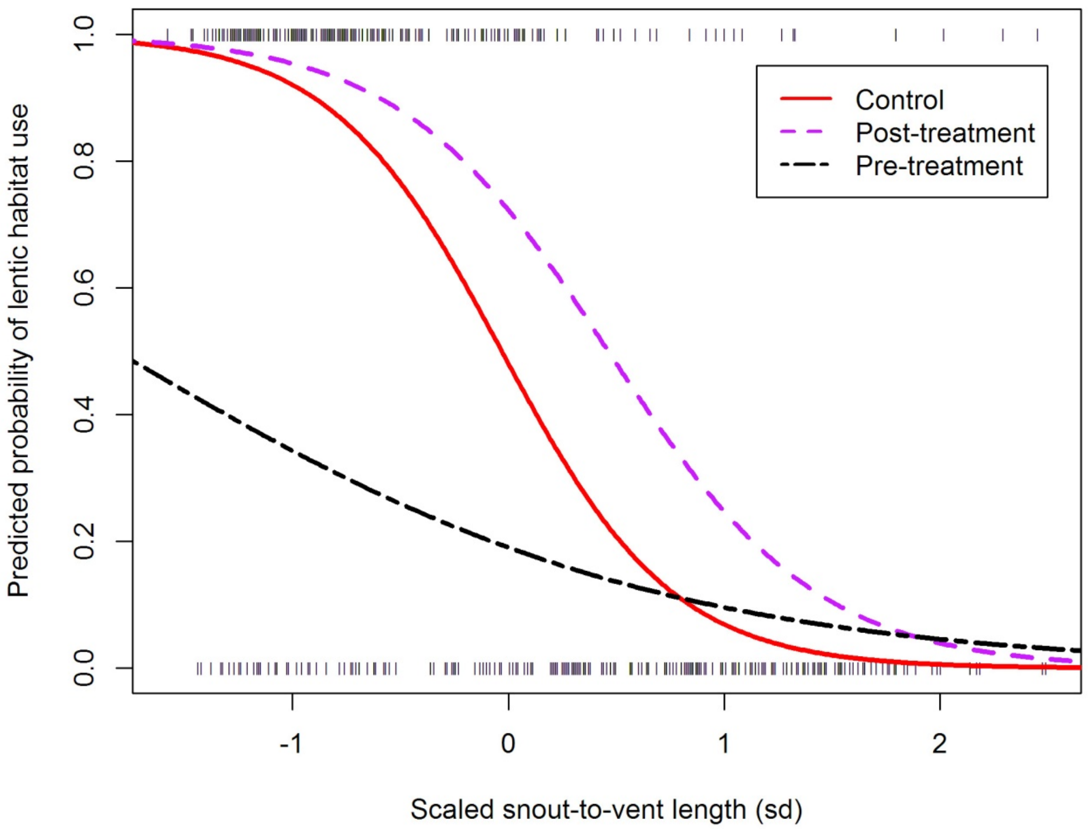

Figure 9. Predicted probability of lentic habitat use in *T. atratus* as a function of scaled snout-to-vent length (0 = an average size snake) and treatment, Echo Lake and Siligo basins, Trinity Alps Wilderness, CA. Model: Bernoulli generalized linear mixed effect.

last few *S. fontinalis* were being removed from Deep Creek Meadow. In Siligo Basin where fish were present, 83 of 92 (90.2%) *T. atratus* stomachs contained a total of 230 individual native amphibian prey while nine stomach samples contained non-native *S. fontinalis*.

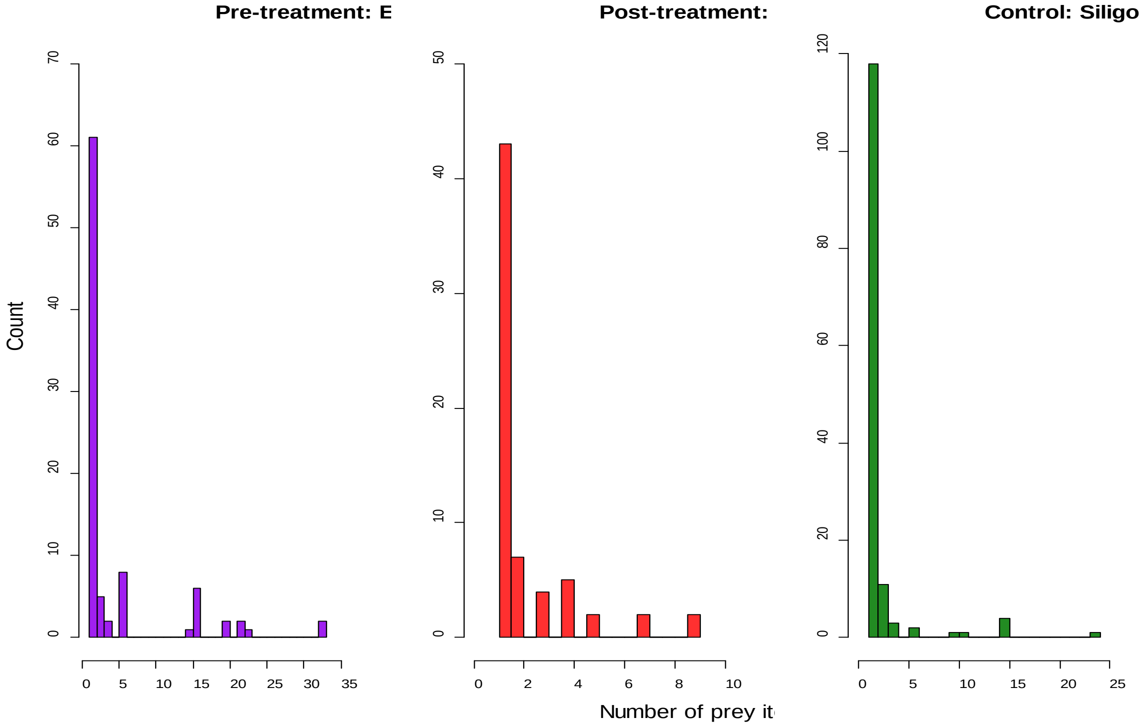

Figure 10. Frequency of stomach samples containing various numbers of prey items in *T. atratus* across Echo Lake and Siligo basins from 2004 through 2006 and from 2016 through 2018, Trinity Alps Wilderness, CA.

Overall, there was a 0.68 probability that the frequency of stomach samples containing native amphibians increased. In Echo Lake Basin prior to fish eradication, the probability that a *T. atratus* stomach sample contained a native was estimated at 0.15 (95% CRI = 0.08 to 0.25). After fish removal, this probability increased to 0.26 (95% CRI = 0.16 to 0.37), which corresponds in an increase in the odds of native amphibian consumption by nearly 1.38 times (95% CRI = 0.67 to 1.67, Figure 12). The most common amphibians consumed across all study years were *R. cascadae* and *P. sierra*.

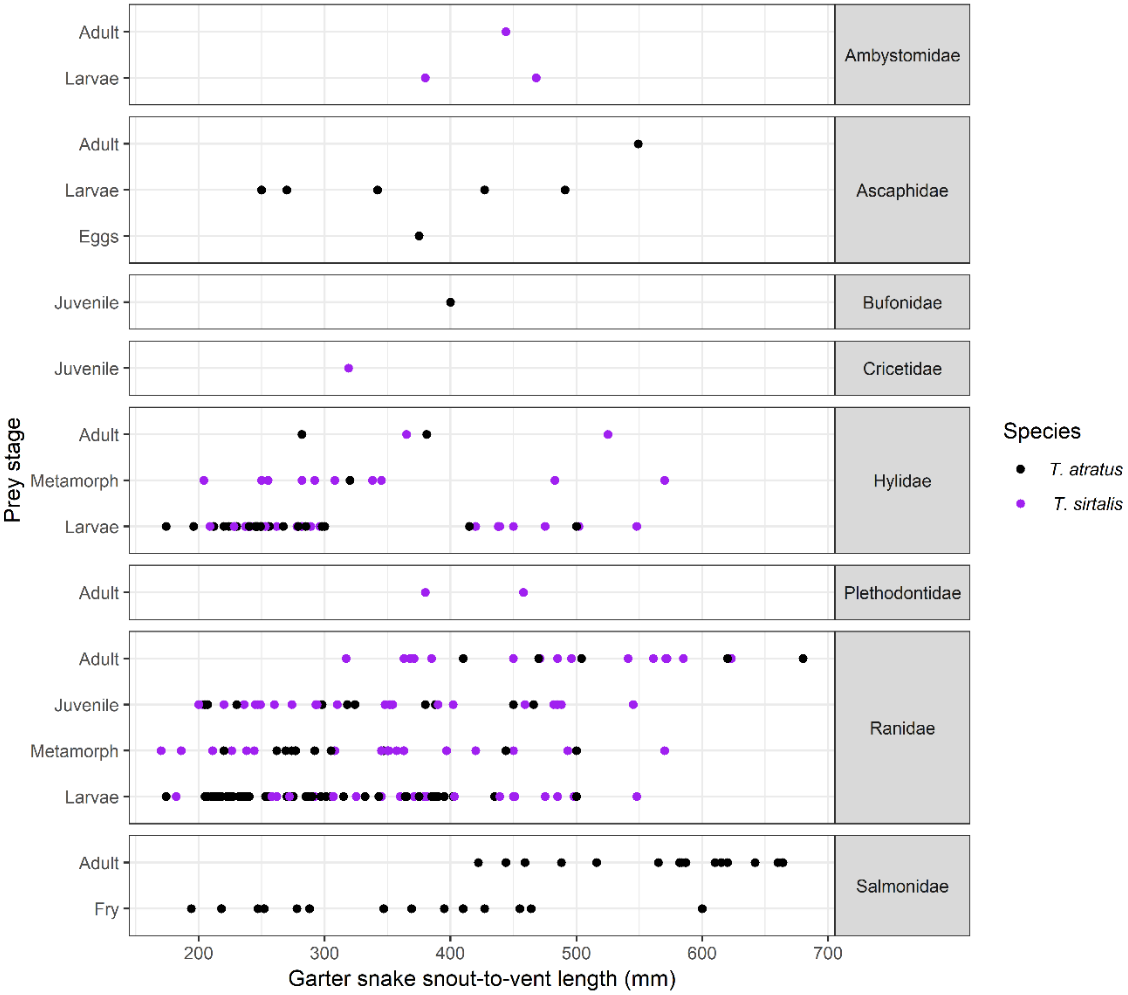

Figure 11. Relationship between snout-to-vent length and prey stage in *T. atratus* and *T. sirtalis*, illustrating the tendency of larger snakes to consume larger prey. *Thamnophis sirtalis* was included to provide a contrast in diet with a sympatric predator. Prey stages are grouped within their respective families for additional clarity. Diet samples were obtained from 2004 through 2006, and from 2016 through 2018, Echo Lake and Siligo basins, Trinity Alps Wilderness, CA.

However, I observed seven predation events on *A. truei* (Coastal Tailed Frog) following fish eradication, totaling eight larvae, one egg strand of three embryos, and one adult.

This constitutes the first documented predation by *T. atratus* on *A. truei* (Figure 11) (Demianew and Macedo, in prep).

Although the probability of palpating a native amphibian from *T. atratus* increased following the eradication of *S. fontinalis*, the mean number of amphibians palpated from individual *T. atratus* did not increase. In fact, there was a 0.95 probability that the average number of amphibians consumed per *T. atratus* was higher prior to fish removal, although the difference was minuscule (mean difference = 0.99; 95% CRI = -0.20 to 2.48). The mean number of amphibians palpated per individual snake was also slightly higher in the adjacent control basin from 2016 through 2018, but only marginally (mean difference = 0.35; 95% CRI = -0.42 to 1.01).

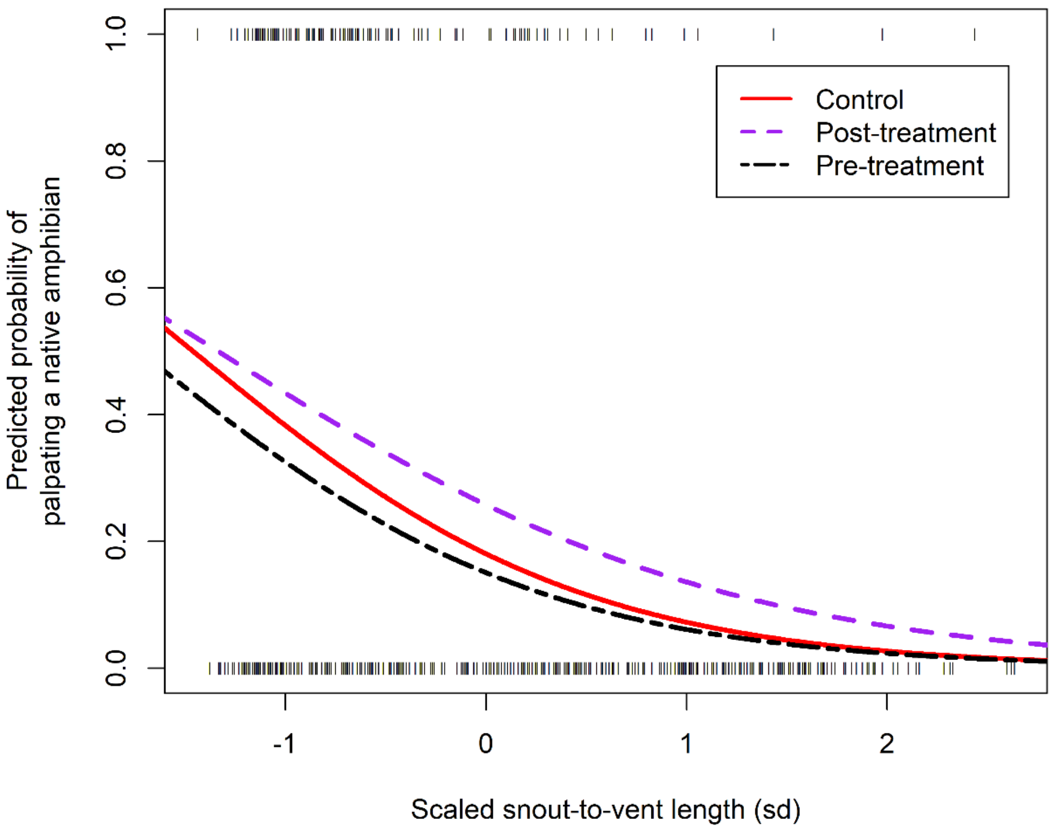

Figure 12. Predicted probability of palpating a native amphibian from *T. atratus* as a function of scaled snout-to-vent length (0 = an average size snake) and treatment in Echo Lake and Siligo basins, Trinity Alps Wilderness, CA. The vertical tick marks represent observed data. Model type: Bernoulli generalized mixed-effect model.

DISCUSSION

Pope et al. (2008) postulated that the introduction of non-native fish into the Klamath Mountains mediated the invasion of *T. atratus* in high elevation habitats, catalyzing hyperpredation on native amphibians. I evaluated the effects of the removal of these non-native fish on a population of *T. atratus* by comparing several aspects of *T. atratus* demography, distribution, and diet to a control population in an immediately adjacent basin. Although I focused my assessment on *T. atratus*, I also examined changes in sympatric populations of *T. sirtalis* to try and understand how trout eradication might also affect this smaller congener in areas where both garter snake species co-occur. I provided two contrasting, although not mutually exclusive, scenarios describing the potential dynamics that might follow eradication of the non-native prey subsidy, both of which were supported by several lines of evidence.

Thamnophis atratus abundance decreased in Echo Lake Basin from 2016 through 2018 consistent with Scenario 1 (Figure 1A), whereas their abundance increased in the control basin. Simultaneously, *T. sirtalis* abundance increased in both basins during this same period. At least part of the decrease in abundance was driven by emigration out of the basin. I observed two instances of *T. atratus* moving out of Echo Lake Basin into areas where fish were not eradicated, also consistent with Scenario 1 (Figure 1A), but I never observed this species moving from the fish-harboring control basin into the treatment basin. Moreover, I observed a within-basin range expansion in *T. atratus* within the treatment basin immediately following fish eradication; a consequence of snakes moving from streams into lentic amphibian breeding ponds both within and outside of their original core-use area (consistent with Scenario 2, Figure 1B). Coinciding with the movements in *T. atratus* from streams to ponds, *T. atratus* displayed other behavior changes following fish removal, including increased rates of predation on native amphibians (consistent with Scenario 2, Figure 1B). The increased predation on amphibians also included the first documented predation on *A. truei*, a species of special concern in California (Thomson et al. 2016). Increased predation on amphibians was driven mostly by neonate and juvenile snakes. Despite these behavioral changes to deal with the eradication of their non-native food subsidy, there were physical consequences of remaining in Echo Lake Basin post-restoration, as indicated by significant reductions in adult *T. atratus* body condition. Together, these results provide convincing experimental evidence to support Pope et al. (2008)'s hyperpredation hypothesis, and they also suggest that in the absence of non-native salmonids, *T. atratus* may be unable to persist at high densities in sub-alpine mountain lake and meadow habitats of the Klamath Mountains.

Demography, Distribution, and Diet

Thamnophis atratus and *T. sirtalis* abundance decreased substantially from 2004 to 2005. This initial decline was possibly driven by a false spring event in 2005, or an early season warming period followed by an extended cold spell (Garwood and Welsh 2007). Cold weather is known to negatively affect garter snakes (Gregory 1977). For instance, light winter snowpack (Shine and Mason 2004) and false springs (Hansen et al.

2015) can result in reduced over-winter and early spring survival. The spring of 2005 corresponds to the second longest *Rana cascadae* breeding season on record in the Trinity Alps (J. Garwood, unpub. data), which was likely driven by a late season snow event (Garwood and Welsh 2007). This false spring could have resulted in snakes waking early and exiting their winter hibernacula into a cold inhospitable environment. This would likely have led to increased physiological stress from an inability to thermoregulate, which in turn would reduce their physiological capacity to acquire and consume prey, thus reducing their survival.

Thamnophis atratus abundance decreased further from 2016 through 2018 following complete eradication of non-native trout throughout Echo Lake Basin. During this same period, their abundance increased in the neighboring control basin where fish were not removed. On the contrary, populations of *T. sirtalis* in both basins increased from 2016 through 2018, with greater increases occurring in the control basin. The mechanism(s) behind these contrasting population trends could be any or all of at least six factors, including: 1) incidental mortality on *T. atratus* resulting from CDFW's fish removal efforts, 2) the removal of non-native trout prey from Echo Lake Basin, 3) *T. atratus* emigration out of Echo Lake Basin, 4) reduced body condition in breeding adult *T. atratus* coupled with 5) the absence of a substantial prey switch to amphibians following trout eradication, and 6) increasing amphibian populations region wide.

Without a doubt, part of the observed decline in *T. atratus* resulted from incidental mortality attributed to CDFW's fish eradication efforts. There were five instances during my study (four in 2016 and one in 2017) where *T. atratus* drowned after being tangled in gill nets deployed to remove non-native fish. These animals, four of which were adult females, were included in the CMR analysis to contribute to annual abundance estimates. Although these deaths were accidental, their contribution to the observed decline is real. Overall, *T. atratus* abundance declined from 37 to 31 animals in Echo Lake Basin from 2016 to 2017, two thirds of that decline can be attributed the known deaths of 4 out of the 5 snakes that died that summer. What is unknown, however, is if those snakes would have died or emigrated out of the basin on their own as a result of the restoration project.

Non-native fish and native amphibians constitute the entire diet of *T. atratus* in the Klamath Mountains (Garwood and Welsh 2007, Pope et al. 2008). In my study basins, fish were common in the largest wetland meadow complexes: Deep Creek Meadow in Echo Lake Basin prior to fish eradication, and Lower Siligo Meadow in Siligo Basin. These sites consist of a mosaic of lentic kettle pools within a braided network of small streams that harbor fish. Over the course of the study the majority of *T. atratus* were detected within these large meadow complexes despite available habitat and higher densities of native amphibians in neighboring sites. Within these meadows, the majority of captures of large snakes occurred in streams that either contain or recently contained non-native fish. Although large snakes have the ability to acquire smaller amphibian prey, they did not appear to do so frequently, and on only a few occasions did I palpate larval or juvenile frogs from the gut of adult *T. atratus*.

Thamnophis atratus experience ontogenetic changes in habitat selection, foraging behavior, and prey selection, which probably reflects an advantage of consuming fewer and larger meals as snakes grow (Lind and Welsh 1994). At lower elevation, the diet of adult *T. atratus* consists mostly of another large stream dwelling prey species, the coastal giant salamander (*Dicamptodon tenebrosus*), even though yellow-legged frog (*Rana boylii*) larvae and juveniles are plentiful (Lind and Welsh 1990, Lind and Welsh 1994). In my study basins, non-native fish are the most abundant large stream-dwelling prey and are thus a likely limiting resource. If this is the case, it would make sense that the absence of fish would lead to starvation and mortality, or encourage animals to seek stream dwelling prey elsewhere, either of which would contribute to the apparent population decline observed in the basin.

On two occasions I observed individual *T. atratus* moving from Echo Lake Basin into fish bearing streams of Lower Siligo Meadow in Siligo Basin. Snakes were never observed moving from Siligo Basin to Echo Lake Basin. These animals, one female and one male, were last captured as juveniles in Echo Lake Basin in 2016, the last year fish were observed in Deep Creek Meadow, and both were recaptured as adults in 2018. Although two observations seem scant, these two snakes represent approximately 6% of all known individuals observed within Echo Lake Basin in 2016. Given the low detection probability in *T. atratus* as a whole (Lind et al. 2005, this study), the true number of animals actually emigrating out of Echo Lake Basin may be much higher.

The elimination of the non-native prey subsidy coincided with a dramatic reduction in the body condition in adult *T. atratus*, but only in the treatment basin. This result is not surprising, however, since fish were the main prey resource in streams where adult *T. atratus* generally forage. On several occasions, I observed *T. atratus* searching for food in the large stream pools of Deep Creek Meadow following fish eradication, despite little to no observed prey. The strong propensity of adult *T. atratus* to forage in streams despite alternative prey in nearby lentic pools is further supported by novel observations of predation on *A. truei*, an alternative stream-dwelling prey resource (Figure 11). In diet studies of *T. atratus* in my study sites and elsewhere, *A. truei* have never been observed in the gut contents of *T. atratus* even though they commonly co-occur (Lind and Welsh 1990, Lind and Welsh 1994, Garwood and Welsh 2007, Pope et al. 2008). This is probably the result of 3 things: 1) availability of preferred prey, 2) the relatively small size and generally nocturnal behavior of *A. truei*, and 3) the strong ontogentic trends in prey selection by *T. atratus*.

As described in this thesis and in other studies, adult *T. atratus* generally forage on large stream dwelling salmonids and amphibians. *Ascaphus truei* is a relatively small amphibian, and although stream dwelling, it is generally nocturnal (Altig and Brodie 1972). These traits likely preclude it from being consumed in large numbers by a generally diurnal garter snake. However, sub-adult or adult *T. atratus* were responsible for five of the seven predation events on *A. truei* in Echo Lake Basin, which began in Deep Creek Meadow immediately after fish eradication. Predation on *A. truei* was not observed in Echo Lake Basin prior to eradication of *S. fonintalis* (Garwood and Welsh 2007, Pope et al. 2008), or in Siligo Basin from 2016 through 2018 despite relatively high densities of this species (A. Macedo, unpub. data). In all but one case, *T. atratus* predation on *A. truei* was concentrated on larvae, which appear relatively more active during the day than adults in this study area (pers. obs.). If adult *T. atratus* are to persist in this environment without preferred non-native fish, *A. truei* are a stream dwelling prey alternative, but they are not a reliable abundant substitute, especially for large snakes. Certain life stages of other amphibians might be more reliable, such as adult *Rana cascadae*, which often spend their summers in streams, although I did not observe increased predation on adult *R. cascadae* in this study.

Although the total number of native amphibians consumed was nearly half that prior to fish eradication, likely a direct result of the decrease in *T. atratus* abundance, the probability of *T. atratus* preying upon native amphibians increased following eradication on non-native trout. This increased rate in native amphibian consumption coincided with a substantial shift in habitat use from lotic streams to lentic pools. This, in addition to the habitat decoupling, was largely driven by juvenile snakes preying on larval and metamorphic frogs. There was almost no observable shift in habitat use in adult *T. atratus* and only a slight predicted increase in their predation on native amphibians. Together, these patterns likely contributed to the absence of a reduction in somatic growth rates in the fishless basin compared to the adjacent positive-control basin. Somatic growth is characterized by the asymptotic growth rate (*k*) and does not reflect the growth rate in adult snakes, but rather neonate and juvenile snakes as they grow rapidly to maturity. These smaller life stages did not seem to be negatively affected by fish eradication since populations of their preferred prey (Anurans) were not removed. Although snakes in these smaller size classes can and do consume non-native fish (Garwood and Welsh 2007, Pope et al. 2008, this study), their diet shows they are not reliant on this resource to the extent adults are. In these habitats, these neonate and juvenile snakes appear fully capable of persisting on the assemblage of available native amphibians, especially larvae, metamorph, and juvenile stages, which consist mostly of as *P. sierra* and *R. cascadae*.

Rana cascadae populations have been decreasing throughout the Klamath Mountains and in other parts of California for much of the last two decades (J. Garwood, unpubl. data, Pope et al. 2014)   However, over the last few years it appears their populations are increasing, at least in the areas where I conducted this study (Demianew and Garwood, in prep). Because neonate and juvenile *T. atratus* and all age classes of *T. sirtalis* rely heavily on native amphibian populations for food, an increase in *R. cascadae* populations might contribute to increases in recruitment across both species of garter snake. In the Sierra Nevada, *T. elegans elegans* is closely tied to the presence of native ranid frogs, and catastrophic population declines in high mountain amphibians resulting from non-native fish has likely led to declines of *T. e. elegans* (Mathews et al. 2002). Thus, it seems reasonable that garter snake populations may increase with increases in their prey populations. The increasing abundance of both species in the control basin and *T. sirtalis* in the treatment basin mirrors the overall apparent increasing trend in sympatric amphibian populations in these basins. The observed trends between predator and prey, however, are based on just a few years of data with estimates that have large uncertainty. Many more years of population monitoring could possibly strengthen the relationship between garter snake abundance and recruitment to the long term trends in native amphibian populations.

The observed distribution in *T. atratus* and *T. sirtalis* not only reflects the space and time variation in their main prey, but it likely also reflects habitat availability within each basin and interspecific competition between the two species. These factors probably affect each garter snake species to varying degrees, with *T. atratus* distribution largely reflecting the distribution of their fish prey and stream habitats, whereas *T. sirtalis* distribution is largely tied to amphibian breeding patches, but only in meadows outside of those occupied by *T. atratus*.

Others have pointed out the strong spatial association between *T. atratus* and non-native fishes (Garwood and Welsh 2007, Pope et al 2008). Eradication of these non-native fish likely decoupled this association, which was reflected in the diffuse distribution of *T. atratus* within Echo Lake Basin following fish removal and their shift in lotic to lentic habitats. Their post-treatment distribution was characterized by a within-basin range expansion of nearly 100% at the 95% isopleth. However, this increase in space use was largely driven by their 2016 distribution, where *T. atratus* were observed in the majority of *R. cascadae* breeding patches throughout Echo Lake Basin, several of which did not appear to be used by *T. atratus* prior to the basin-wide restoration effort. This pattern may have been driven by their pursuit of amphibian prey, but amphibian prey remained abundant in Deep Creek Meadow, the core use area of *T. atratus*, before and after restoration. Their expanded distribution is more likely the consequence of snakes prospecting for fish prey in alternative nearby sites. Recaptures of *T. atratus* in these peripheral lentic breeding patches almost never occurred, likely because they were all fishless and the amphibians present are neither preferred nor consistently available prey. This is exacerbated by the fact that most of these breeding patches are small, they lack permanent stream features that are favored by larger *T. atratus*, and most are susceptible to drought-associated desiccation which has likely affected the region for much of the last seven years.

By 2017 and 2018, the distribution of *T. atratus* contracted substantially, nearly resembling their distribution prior to fish eradication. Regardless of the initial within-basin range expansion and subsequent range contraction, in all years their core use area (50% isopleth) was concentrated within Deep Creek Meadow. In neighboring Siligo Basin, the home range size and distribution in *T. atratus* was relatively unchanged year to year, and the core area of those distributions were consistently concentrated around fish-filled streams and the immediately adjacent Anuran breeding ponds in Lower Siligo Meadow.

The home range size and distribution in *T. sirtalis* varied substantially from year to year within Echo Lake Basin. This was probably driven in part by their small and fluctuating population size, diffuse distribution, and their patchily distributed ephemeral prey base, all of which influence the resulting utilization distribution. The home ranges used in this study were based off all detections of this species. Unfortunately, the total number of detections in a given year was usually very low (Table 2). As such, small changes in the number of detections, which likely results from fluctuations in their population size, would represent a significant change in the proportion of detections used in the home range analysis. Coupled with their relatively diffuse distribution that may reflect their patchily distributed and preferred amphibian prey (Garwood and Welsh

2007, Pope et al. 2008), greater fluctuations in their within-basin range size and distribution through time might be expected compared to the control basin, where their population and prey are more concentrated within fewer sites. This small sample size issue likely does not affect *T. atratus* to the same degree, however, since *T. atratus'* core use area was generally tied to one site throughout the study. Similar to *T. atratus*, *T. sirtalis* distribution and home range sizes in Siligo Basin remained nearly constant throughout the study.

The degree to which the distribution of *T. atratus* shapes that of *T. sirtalis* is not entirely clear. In general, *T. sirtalis* were rarely observed throughout the amphibian breeding ponds in wetland meadows occupied by *T. atratus* (Figure 13), although they were encountered regularly in similar habitats where *T. atratus* were not found. The biggest differences in these habitats were the presence of trout and an extensive network of streams. In meadows where *T. atratus* and *S. fontinalis* co-occur, neonate and juvenile *T. atratus* were typically encountered amongst the archipelago of amphibian breeding ponds where one would expect to also encounter *T. sirtalis*, whereas adult *T. atratus* were almost always observed foraging in streams. Habitat partitioning is a common phenomenon observed in sympatric species within the same guild (MacArthur and Wilson 1967, Shoener 1974), and has been documented in many species of snake (reviewed in Luiselli 2006). Habitat and resource partitioning is evident within the largest size classes between *T. atratus* and *T. sirtalis*. These habitat differences might have evolved to reduce competition where they naturally co-occur at lower elevations, but these differences might also be independent of competition (Shoener 1982).

Regardless of their evolutionary origins, the propensity of *T. atratus* to use stream habitats is not as strong in neonates and juveniles as it is in adults. Although these animals are found commonly at the margin of streams in larger riverine systems at lower elevations (Lind and Welsh 2004, Welsh et al. 2010), smaller *T. atratus* generally occupy ponds in this system, which are relatively rare habitat features at lower elevations.

The difference in habitat use between small and large snakes is possibly a behavioral response to reduce intraspecific competition, or because small snakes can more easily acquire smaller defenseless amphibian prey in pond habitats relative to larger and more mobile fish prey in lotic features. The dense constellations of pond habitats are likely a relatively novel habitat type for *T. atratus*, and their occupation of these habitats put them in direct conflict with *T. sirtalis* in high elevation areas of the Klamath Mountains. In sites where both species were caught within the same year, these garter snakes were almost never caught together on the same day. In 2016 through 2018, I only every observed the two species together in the same water feature on a handful of occasions, and all but one of these occasions were in areas where *T. sirtalis* was the more abundant species. Generally, the aquatic features where they co-occurred temporally were either very large (Echo Lake) or contained high densities of larval and transforming frogs (e.g., Snowmelt Pond), both of which probably help to reduce interference competition. Moreover, I did not find any evidence that *T. sirtalis* moved into Deep Creek Meadow following restoration. Although *T. atratus* declined within this site over the course of this study, many of the remaining snakes shifted their habitat use into the adjacent lentic amphibian breeding ponds, likely intensifying the potential for

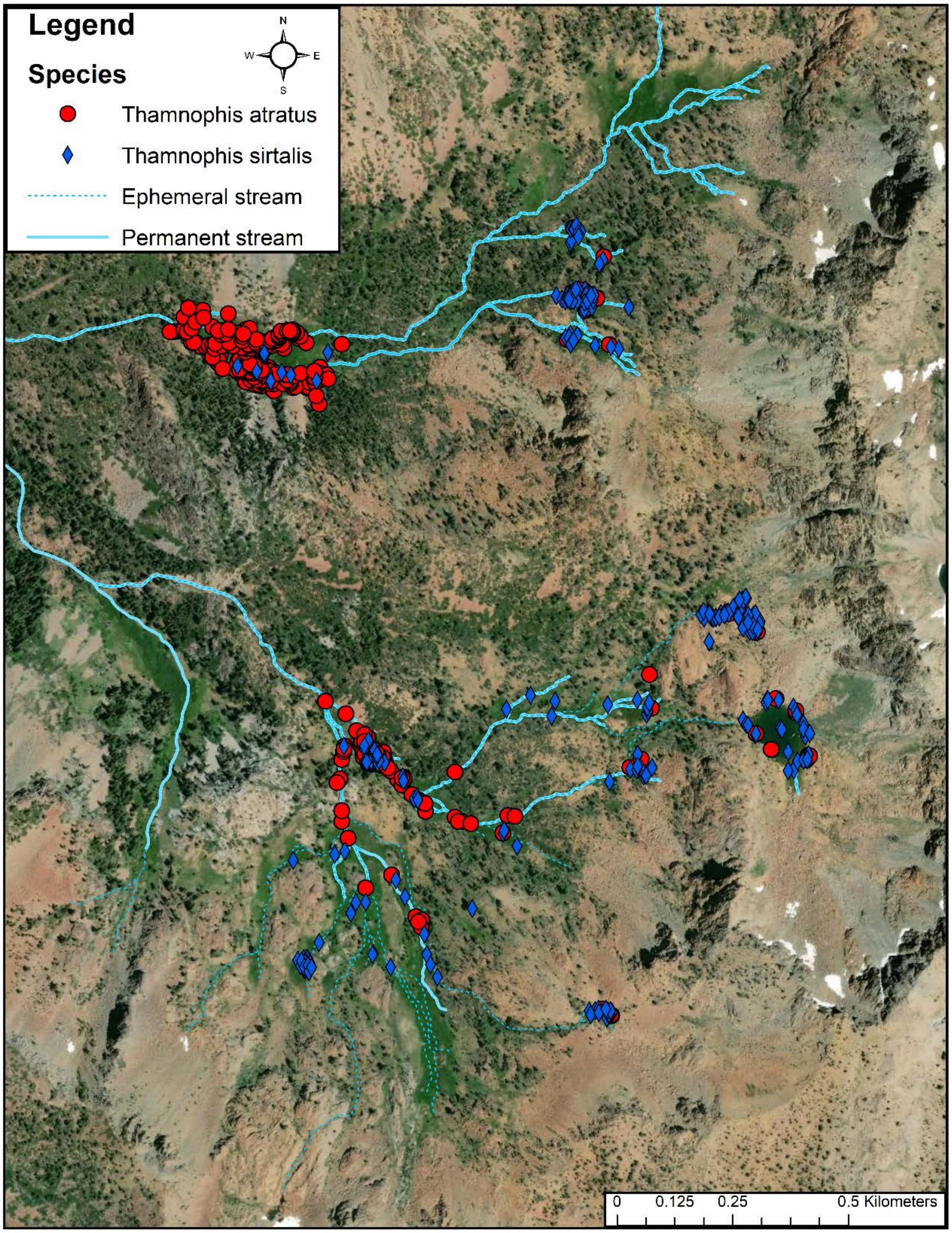

Figure 13. Detections of *T. atratus* and *T. sirtalis* from 2004 to 2006 and from 2016 through 2018, Echo Lake and Siligo basins, Trinity Alps Wilderness, CA.

competitive exclusion of *T. sirtalis*. Together these observations make for a compelling case that *T. atratus* do in fact exclude *T. sirtalis* in areas where they co-occur, but additional research, such as enclosure experiments, would be required to infer causation.

The majority of research on sympatric species of snakes illustrates that they generally partition habitat or prey resources (Arnold 1972, Reinert 1984, Luiselli 2006, Edgehouse et al. 2014). The fact that *T. atratus* and *T. sirtalis* do not partition prey and habitat resources completely is likely the result of recent sympatry, which resulted from non-native fishes mediating the elevational range expansion and increases in abundance of *T. atratus* (Pope et al. 2008). Other sub-species of these snakes are known to exist in sympatry in coastal central California, but unlike here, competitive exclusion is reversed, with *T. sirtalis* apparently displacing *T. atratus* in areas where they co-occur (Edgehouse et al. 2014). Edgehouse et al. (2014) does not provide convincing field data of this negative association, however, but rather provides evidence from a laboratory-based enclosure experiment, the results of which may be confounded by the fact that individuals of *T. siralis* used in the experimental trials were significantly larger (Edgehouse et al. 2014) and thus might have had a competitive advantage. Their contrasting results might also be attributed to the aggressive behavior displayed within the sub-species across their respective ranges. On average, *T. atratus* are larger than *T. sirtalis* in the Klamath Mountains and are much more aggressive in hand. Additionally, compared to other populations of *T. sirtalis* in coastal northern California and central California, these high elevation *T. sirtalis* are relatively docile (pers. obs.). Together, this might contribute to them being competitively inferior in aquatic habitats in my study area. If they had been a competitively superior snake, they may have thwarted the native invasion of *T. atratus* into sub-alpine habitats throughout the Klamath Mountains.

Conclusion

Recognizing the impacts non-native species have on food web structure and ecosystem function is critically important for understanding, managing, and potentially mitigating the impacts of non-native species (Ricciardi et al. 2013). This is especially important in areas that are considered pristine and protected, such as designated wilderness lands, since negative impacts of introduced or invasive species may go unnoticed (Vredenburg 2004). Without intimate knowledge of the role non-native species play in local food webs, formulation of appropriate removal strategies and predictions of their effectiveness will be difficult to accomplish, which might increase the likelihood of unexpected and unintended outcomes following management actions such as habitat restoration and non-native species eradication.

In invasion biology, eradications are a great tool to experimentally test ecological processes involving non-native species’ effects on local food webs (Fukami et al. 2006). Not only can experiments be used to identify direct and indirect effects operating between species within a community, but they can be used to highlight the strength of top-down and bottom-up regulation and the role these processes have in structuring community assemblages (Russell 2011). This thesis provides direct experimental evidence strengthening Pope et al. (2008)’s postulate that non-native trout mediate hyperpredation on native amphibians through increases in abundance of a shared consumer. This thesis also highlights the fact that conservation-based management actions can sometimes yield unpredicted outcomes resulting from unforeseen shifts in food web structure (e.g., novel predation on *A. truei*), despite intimate knowledge of the system prior to restoration. Nevertheless, these short-term community responses and novel interactions contribute to the growing field of invasion biology. In addition, they provide context for future restoration efforts, both in the Klamath Mountains and beyond, while contributing to the ecology and understanding of sympatric predators and their prey.

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APPENDIX A

Appendix A: Superpopulation parameterization of the Jolly-Seber model, modified from Crawford et al. (2018) based on Kéry and Schaub (2012). This example model was used to estimate changes in abundance, survival, per-capita recruitment, and population growth rate in *T. atratus* across two populations in two adjacent basins. The Jolly-Seber model was specified in the jags dialect of BUGS. See Crawford et al. (2018) for a formal model description.

```
sink("ATRATUS.jags")
cat("
   model{

#Survival
         for (i in 1:M) {
                  g[i] <- basin[i]+1
                           for (y in 1:(n1-1)){
                                    phi[i,y] <- phi.g[g[i],y]
         }
   }

         for (u in 1:2){
                  for(y in 1:(n1-1)){
                           phi.g[u, y] ~ dbeta(4,3)
                  }
         }
```

Entry

```
          for (i in 1:M) {
                    for (y in 1:n1) {
                              nu[i,y] <- nu.g[g[i],y]
          }
   }
          for (u in 1:2) {
                    for (y in 1:n1) {
                              ent[u,y] ~ dgamma(1, 1)
                              b[u,y] <- ent[u,y] / sum(ent[u,1:n1])
          }
   }
```

```
#Conditional entry
          for (u in 1:2) {
                    nu.g[u,1] <- b[u,1]
                              for (y in 2:n1) {
                                        nu.g[u,y] <- b[u,y] / (1-sum(b[u,1:(y-1)]))
          }
   }
```

```
#Temporary emigration
          for (i in 1:M) {
                    for (y in 2:n1){
                              gamma[i,y] <- gamma.g[g[i],y]
          }
   }
          for (u in 1:2) {
                    for (y in 2:n1){
                              gamma.eta[u,y] <- gam.mu[u] + gam.eps[u,y]
                              gamma.g[u,y] <- 1/(1+exp(-gamma.eta[u,y]))
                              gam.eps[u,y] ~ dnorm(0,gam.tau[u])
          }
                    gam.mean[u] ~ dunif(0,1)
                    gam.mu[u] <- log(gam.mean[u]/(1-gam.mean[u]))
                    gam.tau[u] <- pow(gam.sd[u],-2)
                    gam.sd[u] ~ dunif(0,5)
   }
```

```
#Capture
            for (i in 1:M) {
                         for (t in 1:n2) {
                                     p[i,t] <- p.g[g[i],t]
            }
    }

            for (u in 1:2){
                        for (t in 1:n2) {
                                    p.eta[u,t] <- p.mu[u] + p.eps[t]
                                    p.g[u,t] <- 1/(1+exp(-p.eta[u,t]))
            }
                        p.mean[u] ~ dunif(0,1)
                        p.mu[u] <- log(p.mean[u]/(1-p.mean[u]))
    }

            for (t in 1:n2) {
                         p.eps[t] ~ dnorm(0,p.tau)
    }

            p.tau <- pow(p.sd,-2)
            p.sd ~ dunif(0,5)

#Inclusion
            psi.rd ~ dunif(0,1)

#State process
            for (i in 1:M){
 #First
            w.rd[i] ~ dbern(psi.rd)
            z.rd[i,1] ~ dbern(nu[i,1])
            f[i,1] <- 0

 # Subsequent
            for (y in 2:n1) {
                        q[i,y-1] <- 1-z.rd[i,y-1]
                        mu1a[i,y] <- phi[i,y-1] * z.rd[i,y-1]
                        mu1b[i,y] <- nu[i,y] * prod(q[i,1:(y-1)])
                        mu1[i,y] <- mu1a[i,y] + mu1b[i,y]
                        z.rd[i,y] ~ dbern(mu1[i,y])
                        avail[i,y] <- gamma[i,y] * z.rd[i,y]
                        f[i,y] ~ dbern(avail[i,y])
```

```
 # Observation process
            for (j in 1:nss[y]) {
                          y.rd[i,(cnss[y]+j)] ~ dbern(p.eff[i,(cnss[y]+j)])
                          p.eff[i,(cnss[y]+j)] <- f[i,y] * p[i,(cnss[y]+j)] * w.rd[i]

                        }
             }
    }

#Recruitment
            for (i in 1:M) {
                        for (t in 1:n1) {
                                    u.rd[i,t] <- z.rd[i,t] * w.rd[i]
            }
    }

            for(i in 1:M) {
                        recruit[i,1] <- u.rd[i,1]
                                    for(t in 2:n1){
                                                recruit[i,t] <- (1-u.rd[i,t-1]) * u.rd[i,t]
                        }
            }

#Abundance
            for (t in 2:n1) {
                        N.loc[t] <- sum(u.rd[1:M,t])
                        B[t] <- sum(recruit[1:M,t])
                        N.loc.Siligo[t] <- inprod(basin[1:M], u.rd[1:M,t])
                        N.loc.Echo[t] <- N.loc[t] - N.loc.Siligo[t]
                        B.Siligo[t] <- inprod(basin[1:M], recruit[1:M,t])
                        B.Echo[t] <- B[t] - B.Siligo[t]
    }

            for (i in 1:M) {
                         N.loc.ind[i] <- sum(u.rd[i, 3:n1])
                         N.loc.alive[i] <- 1-equals(N.loc.ind[i], 0)
    }

            Nsuper.loc <- sum(N.loc.alive[])

    }
    ",fill=TRUE)
sink()
```

APPENDIX B

Appendix B: Eaton and Link parameterization of the von Bertalanffy growth model, modified from Eaton and Link (2011). This example model was used to estimate individual, sex, and basin fixed effects on growth parameters in two populations of *T. atratus*. The von Bertalanffy model was specified in the jags dialect of BUGS. See Eaton and Link (2011) for a formal model description and additional code.

```
sink("THAT_EL.jags")
cat("
model{

        for(i in 1:53){                         # Individuals recaptured 1x
                for (j in 1:1){
                        h[i,j] ~ dnorm(H[i,j],tau.eps)
                        H[i,j] ~ dgamma(P[i,j],lambda)
                        P[i,j] <- lambda*H.m[i,j]
                        H.m[i,j] ~ dunif(150,850)
                                }
                for (j in 2:2){
                        h[i,j] ~ dnorm(H[i,j],tau.eps)
                        H[i,j] <- H[i,j-1]+increment[i,j]
                        increment[i,j] ~ dgamma(P[i,j],lambda)
                        P[i,j] <- (lambda+alpha*sex[i])*abs(H.m[i,j]-H.m[i,j-1])
                        H.m[i,j] <- H.m[i,j-1]+((a+beta0*sex[i])-H.m[i,j-1])*(1-exp(-
                        (k+beta1*sex[i]+beta2*basin[i])*(dslc[i,j]/260)))
                                }
                        }
        for(i in 54:86){                        # Individuals recaptured 2x
                for (j in 1:1){
                        h[i,j] ~ dnorm(H[i,j],tau.eps)
                        H[i,j] ~ dgamma(P[i,j],lambda)
                        P[i,j] <- lambda*H.m[i,j]
                        H.m[i,j] ~ dunif(150,850)
                                }
```

```
for (j in 2:3){
          h[i,j] ~ dnorm(H[i,j],tau.eps)
          H[i,j] <- H[i,j-1]+increment[i,j]
          increment[i,j] ~ dgamma(P[i,j],lambda)
          P[i,j] <- (lambda+alpha*sex[i])*abs(H.m[i,j]-H.m[i,j-1])
          H.m[i,j] <- H.m[i,j-1]+((a+beta0*sex[i])-H.m[i,j-1])*(1-exp(-
          (k+beta1*sex[i]+beta2*basin[i])*(dslc[i,j]/260)))
               }
          }
for(i in 87:97){                         # Individuals recaptured 3x
     for (j in 1:1){
          h[i,j] ~ dnorm(H[i,j],tau.eps)
          H[i,j] ~ dgamma(P[i,j],lambda)
          P[i,j] <- lambda*H.m[i,j]
          H.m[i,j] ~ dunif(150,850)
               }
     for (j in 2:4){
          h[i,j] ~ dnorm(H[i,j],tau.eps)
          H[i,j] <- H[i,j-1]+increment[i,j]
          increment[i,j] ~ dgamma(P[i,j],lambda)
          P[i,j] <- (lambda+alpha*sex[i])*abs(H.m[i,j]-H.m[i,j-1])
          H.m[i,j] <- H.m[i,j-1]+((a+beta0*sex[i])-H.m[i,j-1])*(1-exp(-
          (k+beta1*sex[i]+beta2*basin[i])*(dslc[i,j]/260)))
               }
          }
for(i in 98:99){                         # Individuals recaptured 4x
     for (j in 1:1){
          h[i,j] ~ dnorm(H[i,j],tau.eps)
          H[i,j] ~ dgamma(P[i,j],lambda)
          P[i,j] <- lambda*H.m[i,j]
          H.m[i,j] ~ dunif(150,850)
     }
     for (j in 2:5){
          h[i,j] ~ dnorm(H[i,j],tau.eps)
          H[i,j] <- H[i,j-1]+increment[i,j]
          increment[i,j] ~ dgamma(P[i,j],lambda)
          P[i,j] <- (lambda+alpha*sex[i])*abs(H.m[i,j]-H.m[i,j-1])
          H.m[i,j] <- H.m[i,j-1]+((a+beta0*sex[i])-H.m[i,j-1])*(1-exp(-
          (k+beta1*sex[i]+beta2*basin[i])*(dslc[i,j]/260)))
     }
}
```

```
# Priors and Derived Parameters for Recapture Data

        lambda ~ dunif(0, 10) #individual heterogeneity
        SdOverRootmean <- 1/sqrt(lambda)
        k ~ dunif(0,5) #growth rate
        a ~ dunif(200,1000) #asymptotic length
        tau.eps ~ dgamma(0.001,0.001)
        sd.eps <- 1/sqrt(tau.eps)
        alpha ~ dunif(-1,1) #sex effect on lambda
        beta0 ~ dunif(-500,100) #sex effect on length
        beta1 ~ dunif(-2,6) #sex effect on growth rate
        beta2 ~ dunif(-1.5,2)  # basin effect on growth rate
}
",fill = TRUE)
sink()
```