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Garter Snake (Thamnophis) Natural History: Food Habits and Interspecific Aggression

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GARTER SNAKE (*THAMNOPHIS*) NATURAL HISTORY: FOOD HABITS AND INTERSPECIFIC AGGRESSION

by

Michael J. Edgehouse

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Biology

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2008

ABSTRACT

Garter Snake (*Thamnophis*) Natural History: Food Habits and Interspecific Aggression

by

Michael J. Edgehouse, Doctor of Philosophy

Utah State University, 2008

Major Professor: Dr. Edmund D. Brodie Jr.
Department: Biology

Communication and recognition are closely intertwined and have been well documented in closely related species over the past several decades. These two types of behaviors often will aid in fostering or disrupting coexistence of similar species. Frequently, it is through different diet patterns that similar species will be able to coexist. This study uses data from 1972 through 2006 to demonstrate the diet of *Thamnophis sirtalis*, *T. atratus, T. elegans,* and *T. couchii* throughout their California range of sympatry with *Taricha torosa*. Additionally, an in-depth examination of the diet of *T. sirtalis, T. elegans*, and *T. atratus* was conducted at the Santa Lucia Preserve (SLP) in Monterey County, California. The results of both data sets indicate that when alone *T. sirtalis* and *T. atratus* consume primarily anurans as their main food source. However, when sympatric, *T. atratus* consumes prey such as earthworms and slugs. *Thamnophis sirtalis* and *T. atratus* consume *Taricha torosa* throughout their California range.

The differences of sympatric and allopatric diet of *T. sirtalis* and *T. atratus* led to ask the question; are the snakes utilizing different microhabitats? This study demonstrates that *T. sirtalis* and *T. atratus* prefer the same habitat when alone. In opposition, when together, *T. sirtalis* will frequently (21 of 24 individuals) use aggression to manipulate the spatial occupation of *T. atratus* as well as the position of *T. elegans* at SLP. This behavior is not consistent throughout *T. sirtalis, T. atratus, T. elegans*, and *T. couchii* range in California and appears to be unique to the SLP.

(102)

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CHAPTER 1

INTRODUCTION

Many evolutionary and genetic questions are based on the specific ecology of organisms. Ecological studies and observations are the conduits through which questions on the genetic and evolutionary origins of organisms and their characteristics travel. It is frequently through observation, field experiments, controlled laboratory experiments, and manipulation that researchers are able to develop questions that delve into the origins of an organism's biology. Reptiles, such as lizards and amphibians, have long been ideal organisms for ecological questions, including questions on community assemblage, thermal ecology, and mate choice (e.g. Schall 1977; Jones et al. 1985; Shine 2003). Snakes, however, are historically underrepresented in this body of literature but have recently been advocated as model organisms for evolutionary and ecological studies (Shine and Bonnett 2000). The unique morphology of snakes (lack of limbs), ectothermic nature, abundance, and relative ease of capture have proved useful in ecological studies. Further investigations into the ecology of these unique organisms can provide additional insight into evolutionary studies of snakes.

The generalist nature of garter snakes (*Thamnophis spp.*) makes them sensitive of their environmental surroundings than many other animals. As noted by Ford and Burghardt (1993), garter snakes need to respond to ever changing environmental cues for their survival. For example, the ability to ingest many different categories of prey and having the ability to recognize when certain prey are more abundant or the times of year when a switch needs to be made, requires a keen awareness of environment. Most *Thamnophis spp.* are generalists in diet and habitat (Rossman et al. 1996). A movement from winter hibernacula, across different ecosystems, to habitat reflective of the season exposes garter snakes to many predatory events. The ability for garter snakes to respond to these changing environmental conditions and occupy the habitat most suitable for the time of year requires awareness to environmental cues.

Early studies of snake diets include relatively simple lists of prey ingested with no indication of the importance of any prey category (Carpenter 1952; Hamilton and Pollack 1956; Shine 1986). More recent snake diet literature has focused on prey size relative to snake size in an effort to include the snake's handling and ingestions abilities (Mushinsky et al. 1982; Garcia and Drummond 1988; Greene et al. 1994; Cobb 2004). Both aspects of snake feeding ecology are vitally important. It is the combination of these data that will have impact our understanding of snake ecology and evolution.

Habitat preferences play a major role in snake ecology. Although they are considered to be generalists, there is conflicting data on the habitat preferences of different garter snake species and their close relatives (Carpenter 1952; Pough 1966; Hebrard and Mushinsky 1978). Much of this conflict arises in delineating habitat differences. The resolution among these studies is species occupation along differing niche axes (temperature, food, time of day, etc.) such that different species occupy slightly different habitats (Mushinsky and Hebrard 1977; Mushinsky et al. 1980; Brown and Parker 1982).

The ecology and interactions among *T. sirtalis, T. couchii, T. atratus,* and *T. elegans* are of particular importance to my study as they are all involved in coevolutionary arms race with the California and rough-skinned newt, *Taricha torosa* and *T. granulosa*. These four species of *Thamnophis* have been studied from Vandenburg, CA. north to Campbell River, BC (Brodie et al. 2002; Brodie unpublished data). *Thamnophis spp.* resistance to tetrodotoxin (TTX), a potent neurotoxin, found in their prey *Taricha spp.*, has a factor investigated among this wide range of populations, with the evolution of resistance to TTX and the increase in the TTX levels of the newts have been of particular interest.

Tetrodotoxin is found in many taxa, including all species of *Taricha* (Brodie et al. 1974; Hanifin et al. 2008). Tetrodotoxin binds to a wide array of voltage-gated sodium channels in nerves and muscles, inhibiting action potential propagation (Hille 1992; Narahashi 2001). Tetrodotoxin levels can be extremely high in *Taricha*, making newts from some populations deadly to any organism that tries to ingest them (Brodie 1968; Hanifin et al. 1999). Some species of garter snakes of the genus *Thamnophis* have entered into an arms race with *Taricha*, in which opposing phenotypic traits (snake resistance; newt toxicity) are evolving in response to each other (Brodie and Brodie 1999; Brodie et al. 2002, 2005; Hanifin et al. 2008).

The parallel arms race between garter snakes and newts can best be described as an exemplary study of the geographic mosaic of coevolution. The geographic mosaic theory of coevolution posits that the form of selection between interacting species varies across a landscape with coevolution active in some spots (hotspots) but dormant in others (coldspots). Brodie and Brodie (1999) demonstrated that newts of the genus *Taricha* are in a coevolutionary arms race with some species of garter snakes, *Thamnophis.* Data show that in areas where newts are highly toxic (possess large amounts of TTX) garter snakes are highly resistant to the TTX; this trend of garter snake resistance to TTX is highly variable (Brodie et al. 2002; but see Hanifin et al. 2008). The majority of coevolutionary hotspots occur within the overlapping California range of *Thamnophis* and *Taricha.*

Recent data suggest that another species of garter snake, *T.couchii,* has also entered into an arms race with *Taricha torosa.* Although previous studies had not detected elevated TTX resistance in *T.couchii* (Motychak et al. 1999), Brodie et al. (2005) demonstrated that *T. couchii* from the Cold Springs region of California have evolved elevated resistance to *Taricha torosa*, similar to the resistance found in *T. sirtalis* in response to *Taricha granulosa. Thamnophis sirtalis* and *T.couchii* are distantly related (de Queiroz et al. 2002), which implies that *T.couchii* has evolved TTX resistance independently (Brodie et al. 2005). In contrast to the independent evolution of resistance in *Thamnophis,* some level of toxicity is present in all three species of *Taricha*, as well as *Notophthalmus* and other salamandrids, implying that TTX is ancestral to the group (Brodie et al. 1974, 2005; Yotsu et al. 1990; Yotsu-Yamashita 2001). Independent origins and familial variation of TTX resistance in *Thamnophis spp.*, and ancestral toxicity in *Taricha spp.* dictate the importance of further examining the arms race that is occurring between these two groups.

Resistance to TTX has been found in sympatric species of garter snakes throughout California (Brodie unpublished). Resistance level, however, appears to vary both within and among species. These new findings further stress the importance of dynamics occurring in California in the ongoing arms race between garter snakes and newts. Central California has proven to be especially interesting, with several species of *Thamnophis* showing elevated but varying resistance levels, as well as inter and intrapopulation variance of TTX levels of *Taricha*. These data may result from unique ecological interactions at many levels, both in central California and throughout the overlapping range of *Thamnophis spp.* and *Taricha spp.* Such as habitat partitioning by different species of *Thamnophis*, diet preferences of different species of *Thamnophis*, nad unique aggressive interactions that may foster these changes in preference. My field sites include the Santa Lucia Preserve (SLP) in Central California, Lassen County (LC) in northern California, and Leoni Meadows (LM), in the central sierra of CA. Each site has unique habitat and populations of *Thamnophis* that have the potential for interactions both with other snakes and with *Taricha* stressing the importance in understanding the life history traits of *Thamnophis* when faced with unique ecological situations.

The Santa Lucia Preserve, Monterey County California is a 20,000-ha central coast landscape located approximately 2 to 20 km southwest of Carmel Valley and approximately 10 km east of the Pacific Ocean. The SLP's varied topography includes flatlands, valleys, rolling hills, canyons, and steep ridgelines located within six different watersheds: Hitchcock Canyon, Las Garzas Creek, Potrero Canyon, Robinson Canyon, San Clemente Creek, and San Jose Creek. The SLP also includes 27 man-made stock ponds that are located in either uplands, seasonal drainages, or riparian corridors. The stock ponds and riparian lands attract significant wildlife including the endangered *Ambystoma californiense* and *Rana aurora draytonii* (McCormick personal comm.). Three species of garter snakes are located throughout the SLP, *T. sirtalis, T. elegans,* and *T. atratus* as well as the newt *Taricha torosa*. Several areas throughout the SLP contain multiple combinations of these species, while others only have one species. The areas at SLP, with different combinations and number of species, create the opportunity for unique interspecific interactions.

Lassen County California is a high elevation lake (Eagle Lake) (1555m) located in northern California. Eagle Lake and the surrounding vicinity are the northern most locales in California where sympatry of *T. elegans, T. couchii,* and *T. sirtalis* is known. Although not in the range of the California *Taricha spp.,* Eagle Lake offers the unique opportunity to study the ecological interactions among these three species of *Thamnophis* without the possible influence of TTX. Creating a situation where the three species of *Thamnophis* do not have to alter their food patterns or face the possible trade-offs of ingesting a toxic prey item.

Leoni Meadows, El Dorado Co. CA, is a high elevation meadow located in the central Sierra foothills. *Thamnophis elegans, T. couchii,* and *T. sirtalis* are found throughout LM and the surrounding area. *Taricha torosa* are also found throughout LM. *Thamnophis spp.* resistance and *Taricha torosa* toxicity are variable at LM. A large amount of interspecific variation exists in *Thamnophis* TTX resistance, while the TTX levels of *Taricha torosa* are relatively low when compared to other California locales. The unique combination of varying resistance and a low-level of toxicity provide an opportunity to investigate ecological interactions with factors not found elsewhere.

It is imperative to understand the interactions occurring between *Thamnophis* and *Taricha* to uncover the necessity for resistance to TTX and/or high levels of TTX. A major step in understanding the interactions between these animals is investigating the diet of *Thamnophis spp.* as they co-occur with *Taricha* in the Californian range. Diet data throughout the overlapping range of *Thamnophis* and *Taricha* in California has been collected from 1972 until present. This large data set coupled with diet sampling I have conducted throughout California may provide some insight as to the interactions between *Thamnophis* and *Taricha.*

The focus of my study is two-fold: First, to examine the diet of several *Thamnophis* species as they co-occur with *Taricha* throughout California. Second, to investigate habitat differences and the mechanisms behind these differences at the Santa Lucia Preserve. A detailed diet analysis of *Thamnophis elegans, T. atratus, T. sirtalis,* and *T. couchii* will provide insight to the frequency that these species consume *Taricha torosa*. The question, do *Thamnophis* eat *Taricha* and if so, with what type of frequency, has been pondered for several years. *Thamnophis* resistance to TTX makes consumption of the toxic *Taricha* a possibility. The data to support this possibility is lacking. The goal of this aspect of my study is to investigate if *Thamnophis* eat *Taricha,* and if so how often.

The second aspect of my study, investigating the spatial preferences of *T. sirtalis, T. atratus, T. elegans,* and *T. couchii,* will give insight to unique observations in the field. Collection efforts at SLP revealed unique spatial occupation trends when species were sympatric vs. allopatric. When *T. sirtalis* and *T. atratus* were not at the same pond they occupied the same area, the 5 meters closest to the edge of the pond. When the two species were sympatric, *T. sirtalis* continued to occupy the space closest to the ponds edge, but *T. atratus* would be found far removed from the edge of the water. These trends have led me to the following questions: What are the spatial preferences of these snake species? Is one species dominant over another species? Is there a specific resource or mechanism by which spatial segregation is occurring? The answers to these questions will aid in our understanding of the interspecific mechanisms through which these species are segregating and possibly identify pathways which one species may be more able to consume *Taricha* than the other.

CHAPTER 2

INTERSPECIFIC AGGRESSION OF *THAMNOPHIS* AT THREE LOCALITITES

Introduction

Communication, the transfer of information from one individual to another, and recognition, the discrimination of self from non-self, are closely intertwined and has been well documented in biologically and ecologically similar species over the past several decades (Carpenter 1977; Payne et al. 2004). These two integral behavior characteristics will often aid in fostering or disrupting coexistence of similar species. Coexistence or segregation can be mediated by communication and recognition processes; including interspecific competition, resource partitioning, interspecific territoriality, predation, migration and interspecific aggression. Interspecific territoriality, defense of a limited resource, and interspecific aggression are important mechanisms by which animals defend territories and drive away competitors and can be hooded under the broader term, interspecific interactions. Interspecific interactions are an important ecological mechanism in structuring communities (Hutchinson 1959; Maynard-Smith 1982). Certain communities of desert rodents, *Plethodon* salamanders, ambystomatid salamanders, desmognathine salamanders, and *Anolis* lizard have been structured by interspecific interactions (Kleeberger 1984; Hess and Losos 1991; Griffis and Jaeger 1998; Lancaster and Jaeger 1995; Smyers et al. 2002; Pinter-Wollman et al. 2006).

Plethodon salamanders have been shown to use aggressive displays toward other species. Lancaster and Jaeger (1995) have shown that the size of the individuals involved is an important variable in interspecific interactions. Adults of one species of salamander (*P. cinereus*) defend their territories, including touching and biting, against juveniles of a larger species (*P. glutinosus*). The age class difference between the two species equalizes the same age class size differences. Interspecific interactions can also render one species more prone to local exclusion or extinction. Griffis and Jaeger (1998) have shown that *P. shenandoah* is more extinction prone because of interspecific territoriality with *P. cinereus*. *Plethodon cinereus* occupies a habitat that is less prone to desiccation during fire and drought and defends it from invading *P. shenandoah*, rendering that species more prone to extinction.

Snake communities also segregate or coexist on the basis of interspecific interactions. Olson and Warner (2001) (also see Kjoss and Litvaitis 2001) found that a community of *T. sirtalis* and *C. constrictor* coexisted based on food partitioning (*T. sirtalis* eating mainly birds and *C. constrictor* eating mainly rodents). Resource partitioning is not the only mechanism by which snake communities may coexist, *Thamnophis* species that occur in sympatry may have increased competition based on similarities in body size, diet, and general habits. Often times this competition for space or food can lead to segregation or local extinction (Reichenbach and Dalrymple 1980; Griffis and Jaeger 1998; Olson and Warner 2001; Smyers et al. 2002; Luiselli 2006).

This study focuses on several snake communities throughout California. The 2005 field-work revealed that *Thamnophis spp.* from the Santa Lucia Preserve (SLP), Monterey Co. CA, were segregating at the species level. During collections it was noted that *T. sirtalis* were found near water at certain locales and *T. atratus* were found far removed from water at these same locales. Subsequently, *T. atratus* were found at certain ponds without *T. sirtalis* only at the waters edge. The difference in *T. atratus* spatial occupation at allopatric and sympatric ponds has led to several questions. What is the preferred habitat of *T. sirtalis* and *T. atratus*? Is one of the species dominant over the other at SLP, if so which one is dominant? What are the mechanisms by which one of the species is dominant? Is there a resource responsible for the interspecific interaction that is being observed? Is the pattern observed at SLP evident at other localities?

Methods

General Animal Collection

Snakes were collected by hand from three California localities: Santa Lucia Preserve, Monterey County, Lassen County, and Leoni Meadows, El Dorado County. Upon collection, the following measurements were recorded for each animal if possible; snout vent length (SVL), mass (grams), and sex. Animals were uniquely ventrally clipped for identification and were housed individually in bags in a temperature control cooler and watered once a day for five days prior to the start of each behavioral trial.

General Experimental Methods

At each of the three study sites ten 4m x 1m x 0.45m enclosures made with black half centimeter weatherproof nylon mesh were utilized to determine microhabitat preference. Enclosures were marked each meter and set 1 m in water and 3 m out of water. One cover object (0.3m x 0.3m x 12.5mm Styrofoam®) was provided on the ground in the meter farthest from the water (zone 1) (Fig. 1). Each trial consisted of a 24-hour period with one animal in the enclosure. Eight observations of position, movement, and behavior were recorded for each snake during each trial. Data were recorded at 700, 800, 1000, 1200, 1400, 1600, 1800, and 1900 hours, from a distance of approximately 20 meters to avoid observer influence and observations were repeated as above for trials with two snakes in the chamber. At each observation the snake's position was recorded as 1 (zone farthest from water) 2, 3, or 4 (zone in water) (Fig. 1), depending on which zone most of the snake's body was in. If an animal was directly between two zones, the head of the snake was used to determine the zone. Instances of aggressive behavior (during trials with more than one snake), such as hissing, biting, chasing, and changes in body morphology (head flattening) was recorded. Biting often occurred in succession with 2-3 directed strikes occurring rapidly in a row. Each sequence of strikes was counted as 1 bite. More than one aggressive behavior was recorded as observed. For example, an obvious head flattening followed by 3 strikes was counted as 1 head flatten and 1 bite.

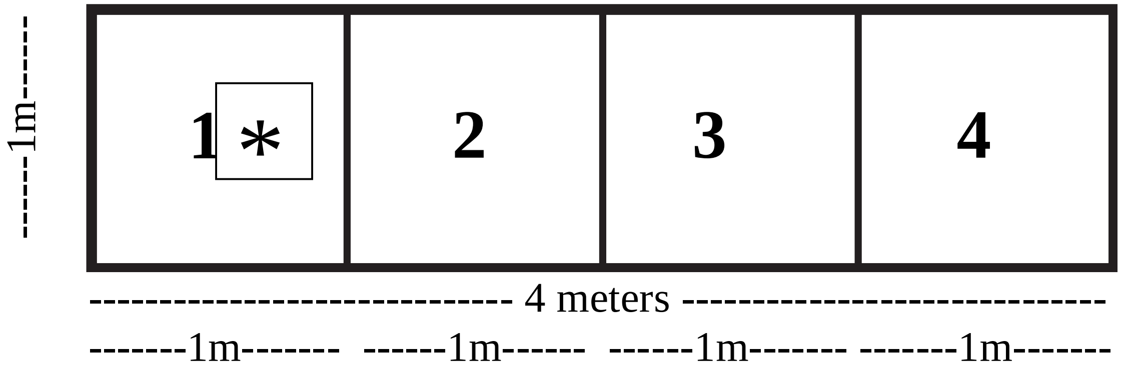

Fig. 1. Behavior test chamber diagram. Enclosures were 4 meters long, with 1-meter delineations, by 1 meter wide, by .45 meters high. Each 1-meter zone was assigned numbers 1,2,3, or 4. Zone 1 was farthest from water and contained one 120cm x 120cm x 1cm Styrofoam cover object, zone 4 was in the water. Snakes were introduced into the enclosures in zone 1.

Analysis

Data were analyzed using positional graphing and chi-square tests for homogeneity of proportions. The zone usage of each snake was recorded. The preferred zone was determined to be the zone the snake was in during the majority of observations. If equal time was spent in multiple zones the preferred zone was split accordingly. Figures were constructed by graphing the percentage of animals preferring each zone. Chi-square tests for homogeneity were used to evaluate the relationship between the numbers of snakes of each species in their preferred zone, and to determine if the addition of another snake had an effect on spatial positioning.

Santa Lucia Preserve (SLP)

Animals from SLP were collected using the above general animal collection protocol. Snakes from ponds where only one species had been observed (allopatric ponds) and ponds where multiple species have been observed during past collections years (sympatric ponds) were targeted for animal collection. Pond 234, a *T. atratus* allopatric pond was used as the primary collection site for *T. atratus*. Golf Course Pond, a *T. sirtalis* allopatric site was targeted as the primary collection site for *T. sirtalis*. Morse Lake and Wetlands, where *T. sirtalis, T. atratus,* and *T. elegans* occur in sympatry, were targeted as collection sites for all three species. Trials were conducted on the southeast corner of the managed wetlands at SLP. This site was chosen to conduct behavior trials because of the shallow water; this enabled the observer to position himself at multiple angles to the enclosure 20 meters away.

After animal collection in 2005, snakes were haphazardly assigned to trials. Ten *T. atratus* vs. *T. atratus* trials were conducted starting on 03 May 2005. These trials followed the general experimental methods protocol described. These trials consisted of placing one *T. atratus* in each enclosure for 24 hours. Upon completion of this 24-hour period another *T. atratus* was then added and observations were again recorded for 24 hours. Upon completion of 20 *T. atratus* vs. *T. atratus* trials, 20 *T. sirtalis* vs. *T. atratus* trials were conducted starting on 06 May 2005. These trials consisted of placing one *T. sirtalis* in each enclosure for 24 hours and following the same protocol as above. Upon completion of this 24-hour period a *T. atratus* was then added and observations were again recorded for 24 hours.

Twenty *T. atratus* vs. *T. sirtalis* trials were conducted starting on 09 May 2005. These trials consisted of placing one *T. atratus* in each enclosure for 24 hours. Upon completion of this 24-hour period a *T. sirtalis* was then added and observations were again recorded for 24 hours.

The final set of trials conducted in 2005 was *T. sirtalis* vs. *T. sirtalis*, starting on 12 May 2005. These trails consisted of placing one *T. sirtalis* in the enclosure for 24 hours. Upon completion of this 24-hour period another *T. sirtalis* was added to the enclosure and observations were recorded for 24 hours. The use of animals more than once in the 2005 trials had no effect on behavior or results.

The data from 2005 showed that different spatial occupations were occurring between *T. sirtalis* and *T. atratus*. It appeared that *T. sirtalis* was causing *T. atratus* to change its spatial occupation sometimes through physical manipulation, but *T. atratus* had no effect on the position of *T. sirtalis*. Because of these results, several trials were omitted in 2006, including *T. atratus* and *T. sirtalis* with conspecifics. As well as *T. sirtalis* occupying the enclosure first and adding *T. atratus*.

Animals in 2006 were assigned to trials with matching SVL as close as possible. Thirteen *T. atratus* vs. *T. sirtalis* trials were conducted starting on 26 May 2006. As seen in 2005, these trials consisted of placing one *T. atratus* in each enclosure for 24 hours. Upon completion of this 24-hour period a *T. sirtalis* was added and observations were again recorded for 24 hours.

Thirteen *T. elegans* vs. *T. sirtalis* trials were conducted starting on May 29, 2006. These trials consisted of placing one *T. elegans* in each enclosure for 24 hours. Upon completion of this 24-hour period a *T. sirtalis* was then added and observations were again recorded for 24 hours.

Data for 2005 and 2006 trials were combined for analysis.

Lassen County (LC)

Animals from LC were collected using the general animal collection protocol between 01 July 2005 and 04 July 2005. Snakes were collected from two localities in the Eagle Lake vicinity. *Thamnophis sirtalis* were taken from Feather Lake (N 40°32.88, W 121°1.28), *T. couchii* were taken from the Devils Corral (N 40°23.65, W 120°46.66), the confluence of the Susan River, Willard Creek, and Williams Creek all 3 in Lassen Co.

Trials were conducted as described in general experimental methods at a seasonal pond in Lassen National Forest (N 40°30.50, W 120°55.21). Twenty *T. sirtalis* vs. *T. couchii* trials were conducted. These trials consisted of placing one *T. sirtalis* in each enclosure for 24 hours. Upon completion of this 24-hour period a *T. couchii* was then added and observations were again recorded for 24 hours.

Twenty *T. couchii* vs. *T. sirtalis* trials were conducted. These trials consisted of placing one *T. couchii* in each enclosure for 24 hours. Upon completion of this 24-hour period a *T. sirtalis* was then added and observations were again recorded for 24 hours.

Conspecific trials were also conducted at LC. Twenty trials of *T. couchii* vs. *T. couchii* were conducted. These trials consisted of placing one *T. couchii* in each enclosure for 24 hours. Upon completion of this 24-hour period a *T. couchii* was then added and observations were again recorded for 24 hours. Twenty trials of *T. sirtalis* vs. *T. sirtalis* were conducted. These trials consisted of placing one *T. sirtalis* in each enclosure for 24 hours. Upon completion of this 24-hour period a *T. sirtalis* was then added and observations were again recorded for 24 hours.

Leoni Meadows (LM)

Animals from LM were collected using the general animal collection protocol between 14 June 2006 and 16 June 2006. Snakes were collected from two localities in the Leoni Meadows vicinity. *Thamnophis sirtalis* were collected from Leoni Meadow (N 38°36.37, W 120°30.47), *T. couchii* and *T. elegans* were collected from Dogtown Creek (N 38°36.2240, W 120°26.1500) both in El Dorado County. Trials were conducted at a permanent pond in the southwest corner of Leoni Meadow.

Trials were conducted as described in general experimental methods. Five trials of each *T. couchii* vs. *T. sirtalis* were conducted. These trials consisted of placing one *T. couchii* in each enclosure for 24 hours. Upon completion of this 24-hour period a *T.*

sirtalis was then added and observations were again recorded for 24 hours. Five trials of *T. elegans* vs. *T.couchii* were conducted. These trials consisted of placing one *T. elegans* in each enclosure for 24 hours. Upon completion of this 24-hour period a *T. couchii* was then added and observations were again recorded for 24 hours. Five trials of *T. sirtalis* vs. *T. elegans*, were conducted. These trials consisted of placing one *T. sirtalis* in each enclosure for 24 hours. Upon completion of this 24-hour period a *T. elegans* was then added and observations were again recorded for 24 hours. Snakes were not used more than once at LM. The trial number was set at five because it was obvious from the results that the snakes were not having influence on each other's position and the number of snakes available was limited.

Results

Santa Lucia Preserve (SLP)

Thamnophis atratus

In every series of trials with a single *T. atratus* in the test chamber, the snake occupied zone 4 (located directly in the water) more often than expected (24 of 31 snakes preferred zone 4, Fig. 2). Introducing a second *T. atratus* to the test chamber did not cause the initial *T. atratus* to shift zones, it continued to occupy zone 4 more than expected (70% of snakes continues to prefer zone 4, Fig. 3). The two *T. atratus* in the test chamber did not occupy significantly different zones (χ^2=2.125, p=0.55) (Fig. 3). No aggression between the two animals was observed.

Two trials were conducted by adding *T. elegans* to *T. atratus.* Although only a few trials were conducted, the addition of *T. elegans* to the test chamber did not cause *T.*

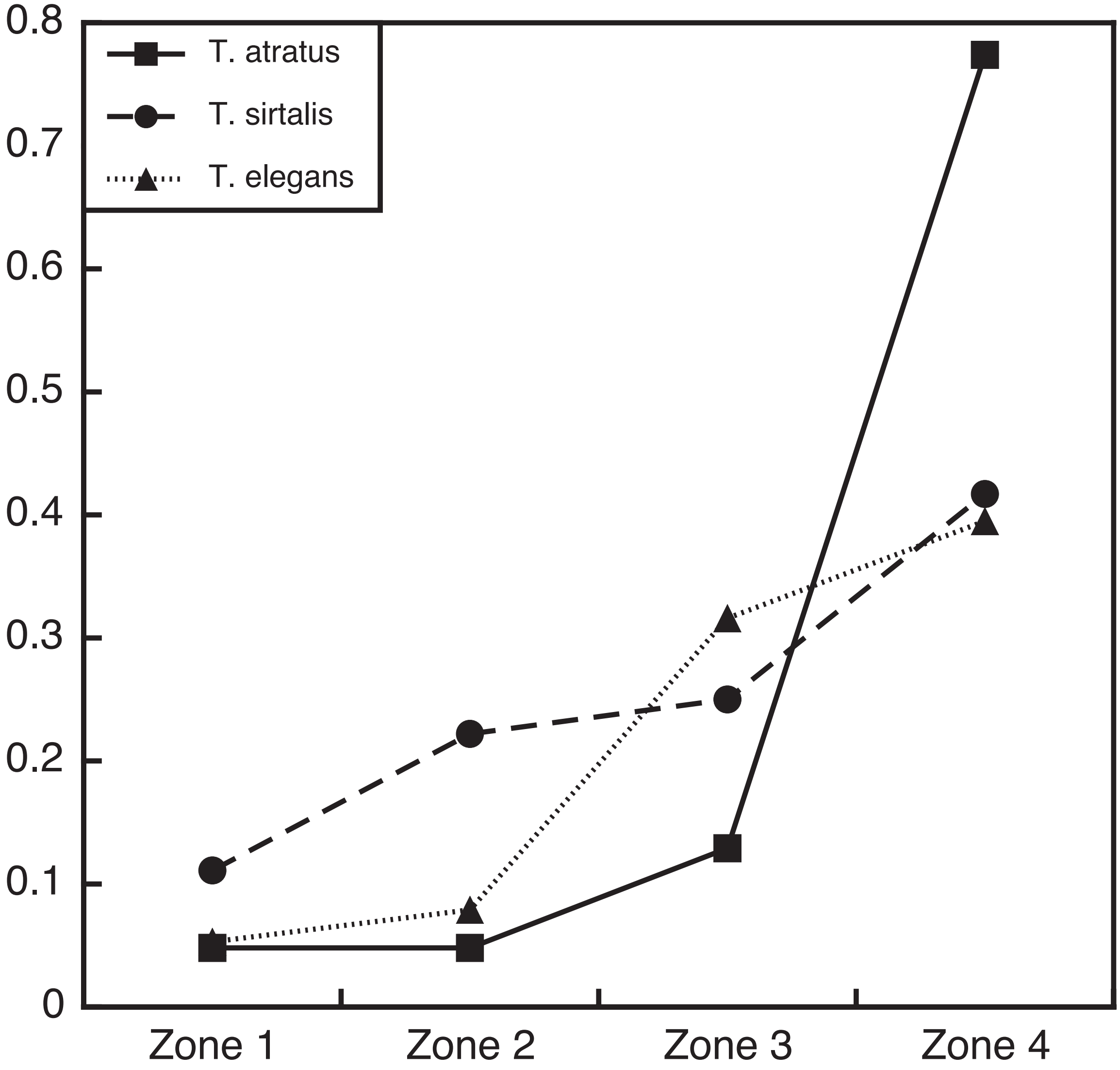

Fig. 2. Percentage of animals from each species in preferred zone from Santa Lucia Preserve when alone.

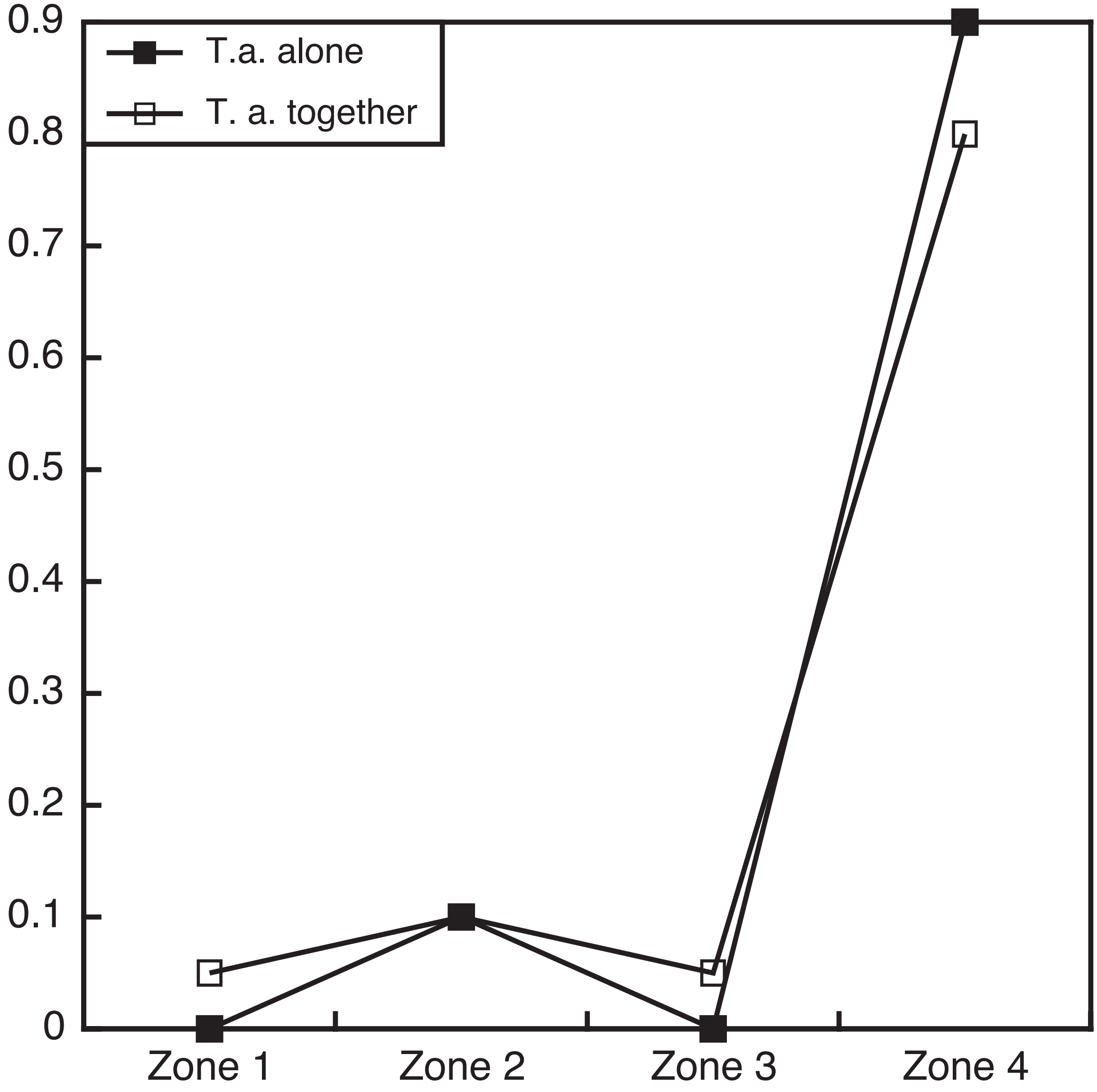

Fig. 3. Percentage of each species in preferred zone for *T. atratus* vs. *T. atratus* trial at Santa Lucia Preserve. *Thamnophis atratus* did not change habitat preference after addition of *T. atratus*. *Thamnophis atratus* and *T. atratus* occupied similar zones when together ($p<0.05$). Preferred zone for *T. atratus* is the average number of snakes in each zone.

atratus to shift its location. *Thamnophis atratus* and *T. elegans* also appear to occupy the same zones.

When *T. sirtalis* was introduced to the test chamber, *T. atratus* shifted their location (Fig. 4). *Thamnophis atratus* spent less time than expected in zone 4 (3 of 24 snakes occupied zone 4), and more time than expected in zone 1 (11.8 of 24 snakes occupied zone 1) (Fig. 4), located farthest from the water, (χ^2=19.862, $p<0.01$). *Thamnophis sirtalis* and *T. atratus* occupied significantly different zones when together (χ^2=23.482, $p<0.01$) (Fig. 4). Most of the *T. sirtalis* used in these trials were observed to exhibit aggression (21 of 24). Thirty-seven aggressive displays (32 head flatten, 5 strikes) were observed from 21 different *T. sirtalis*.

Thamnophis elegans

In every series of trials with a single *T. elegans* in the test chamber, they occupied zone 3 and 4 more often than expected (13.5 of 16 snakes preferred zones 3 or 4)(Fig. 2). Introducing a second *T. elegans* to the test chamber did not cause the initial *T. elegans* to shift zones. The two *T. elegans* in the test chamber did not occupy different zones (5.5 of 6 snakes occupied zone 4). No aggression was observed between the two animals.

When *T. sirtalis* was added to the test chamber, *T. elegans* changed its preferred zone (11 of 13 snakes preferred zone 1, χ^2=18.373, $p<0.01$) (Fig. 5). *Thamnophis elegans* and *T. sirtalis* occupied different zones of the test chamber *(T. elegans* =85% zone 1, *T. sirtalis* = 50% zone 1, 46% zone 4) (Fig. 5). Most of the *T. sirtalis* used in these trials were observed to exhibit aggression (11 of 13). Thirty-four aggressive displays were observed between *T. elegans* and *T. sirtalis* (29 *T. sirtalis*, 20 head flatten, 9 strikes; 5 *T. elegans*, 4 head flatten, 1 strike). The 29 *T. sirtalis* aggressive displays

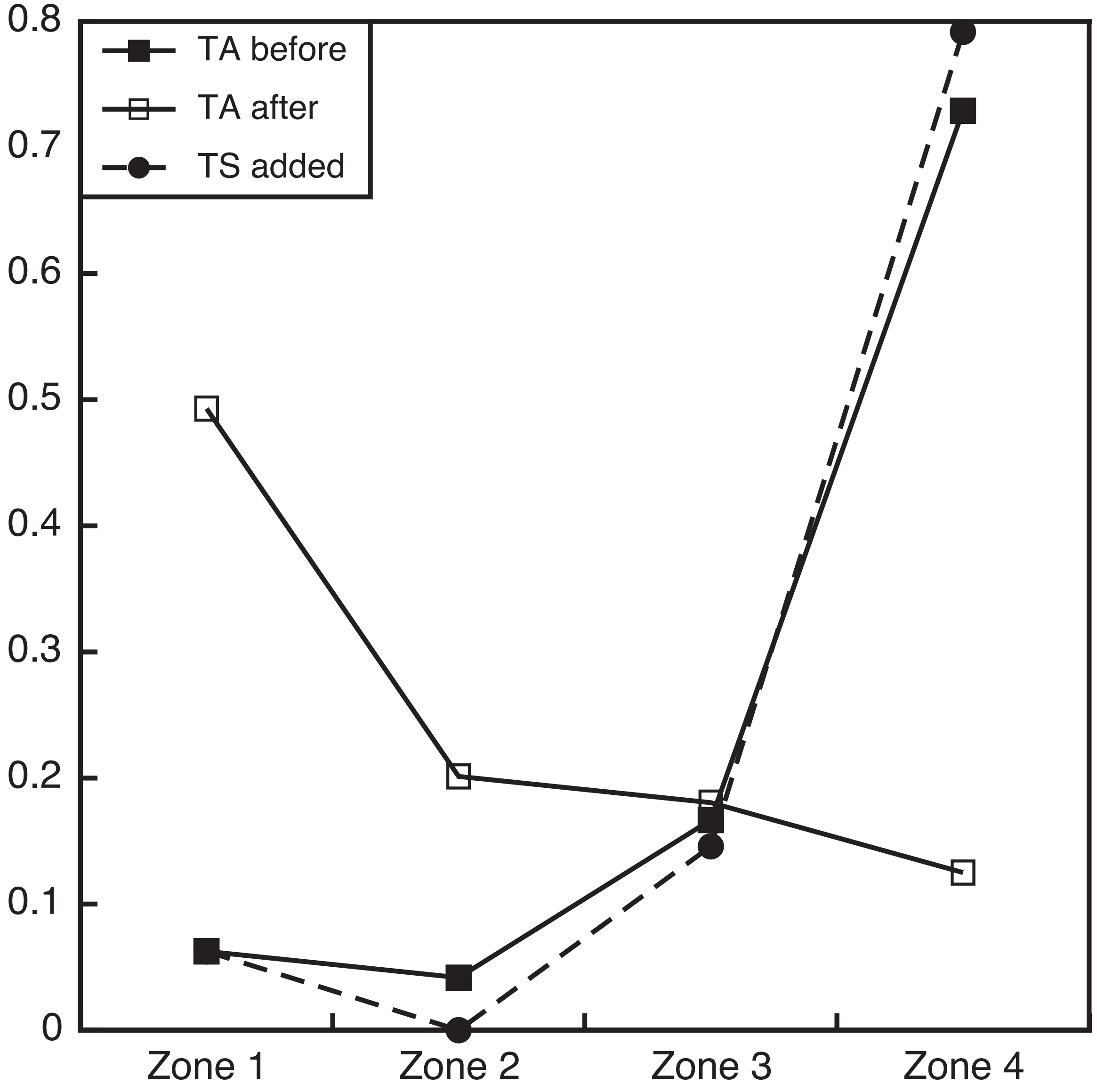

Fig. 4. Percentage of each species in preferred zone for *T. atratus* vs. *T. sirtalis* trial at Santa Lucia Preserve. *Thamnophis atratus* changed habitat preference after addition of *T. sirtalis* (p< 0.001). *Thamnophis atratus* and *T. sirtalis* occupied different zones when together (p<0.001).

were from 11 different animals. The 5 *T. elegans* aggressive displays were from 3 different animals.

Thamnophis sirtalis

In every series of trials with a single *T. sirtalis* in the test chamber, the snake occupied zone 4 more than expected (7.5 of 18 snakes preferred zone 4) (Fig. 2). Introducing a second *T. sirtalis* to the test chamber did not cause the initial *T. sirtalis* to shift zones (χ^2=3.674, p=0.3)(Fig. 6). The two *T. sirtalis* in the test chamber did not occupy significantly different zones (χ^2=6.092, p=0.11) (Fig. 6). Half of the *T. sirtalis* used in these trials were observed to exhibit aggression (5 of 10). Six aggressive displays were observed from 5 different animals (6 head flatten).

When *T. atratus* was added to the test chamber, *T. sirtalis* did not change its' location (χ^2=3.733, p=0.3) (Fig. 7). *Thamnophis sirtalis* and *T. atratus* did occupy different zones. Fifteen aggressive displays were observed from 8 different *T. sirtalis* (10 head flatten, 5 strikes).

Lassen County (LC)

Thamnophis couchii

In every series of trials with a single *T. couchii* in the test chamber, they occupied zone 1 and zone 4 more often than expected (21.5 of 29 snakes preferred zones 1 or 4, Fig. 8). Introducing a second *T. couchii* to the test chamber did not cause the initial *T. couchii* to shift zones (80% of snakes preferred zones 1 and 4, χ^2=3.048, p=0.38 Fig. 10).

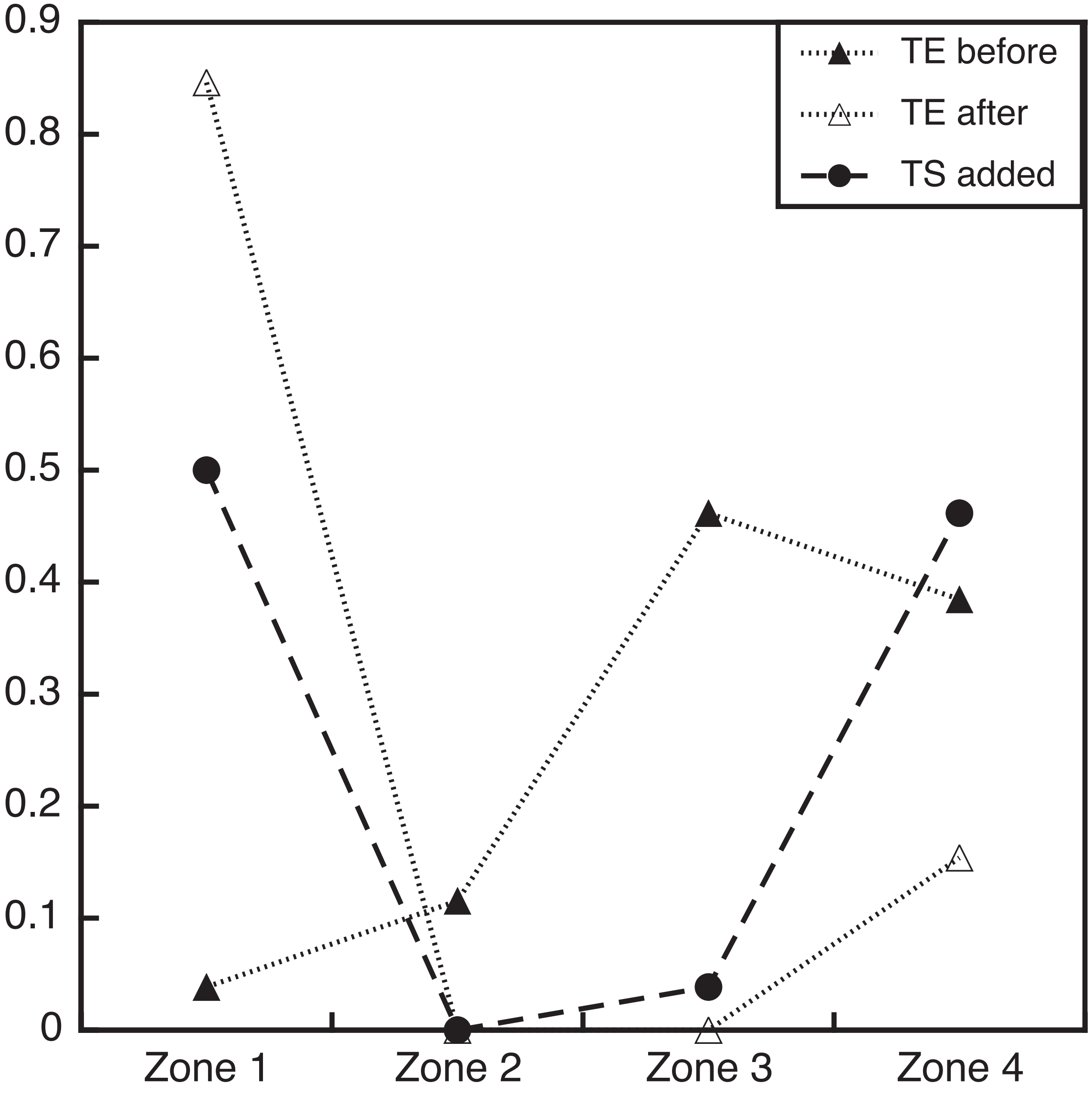

Fig. 5. Percentage of each species in preferred zone for *T. elegans* vs. *T. sirtalis* trial at Santa Lucia Preserve. *Thamnophis elegans* changed habitat preference after addition of *T. sirtalis* ($p < 0.001$). *Thamnophis atratus* and *T. sirtalis* occupied similar zones when together.

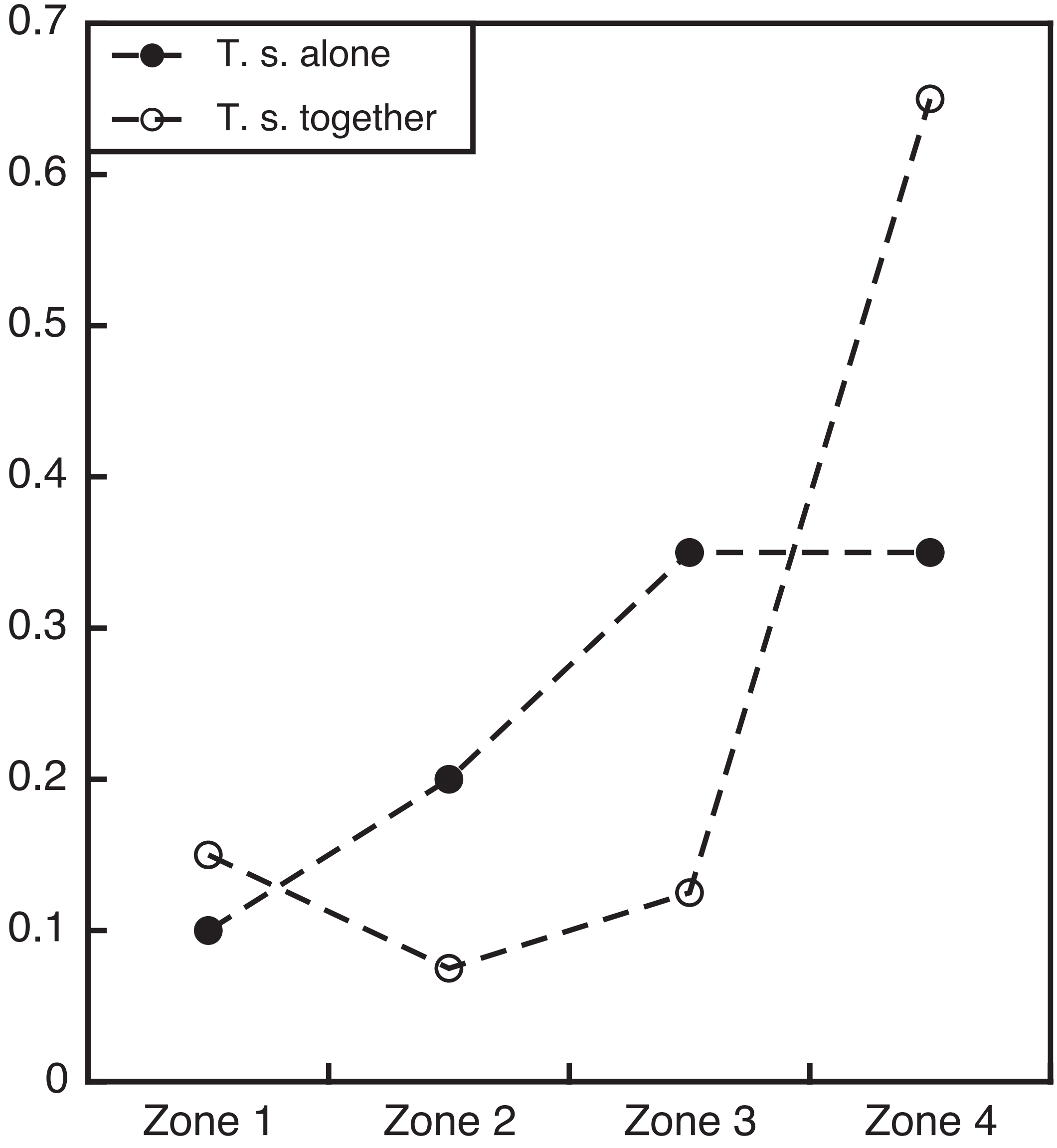

Fig. 6. Percentage of each species in preferred zone for *T. sirtalis* vs. *T. sirtalis* trial at Santa Lucia Preserve. *Thamnophis sirtalis* did not change habitat preference after addition of *T. sirtalis* (p> 0.05). *Thamnophis sirtalis* and *T. sirtalis* occupied similar zones when together (p<0.05). Preferred zone for *T. sirtalis* is the average number of snakes in each zone.

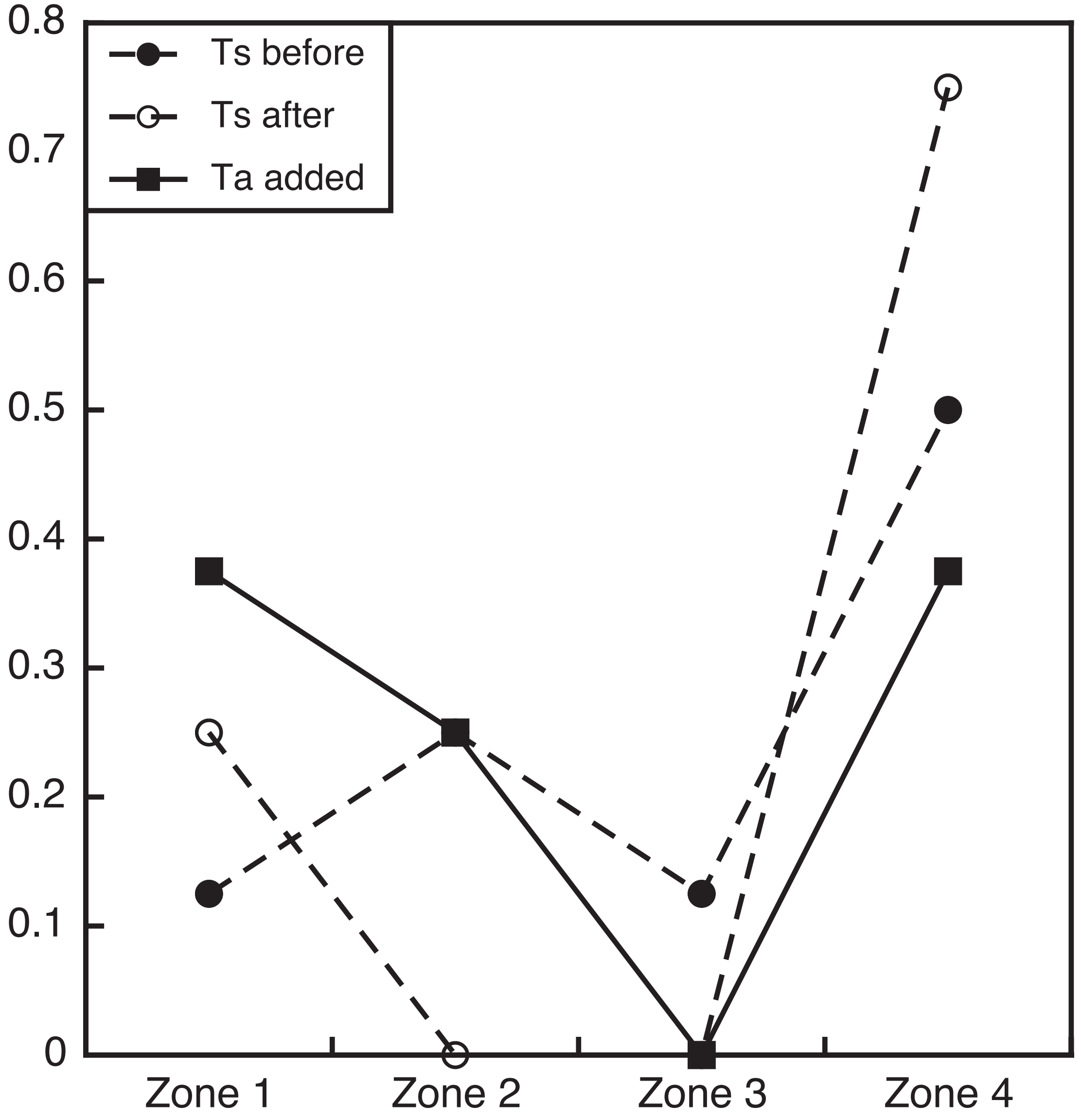

Fig. 7. Percentage of each species in preferred zone for *T. sirtalis* vs. *T. atratus* trial at Santa Lucia Preserve. *Thamnophis sirtalis* did not change habitat preference after addition of *T. atratus* (p> 0.05). *Thamnophis sirtalis* and *T. atratus* occupied different zones when together.

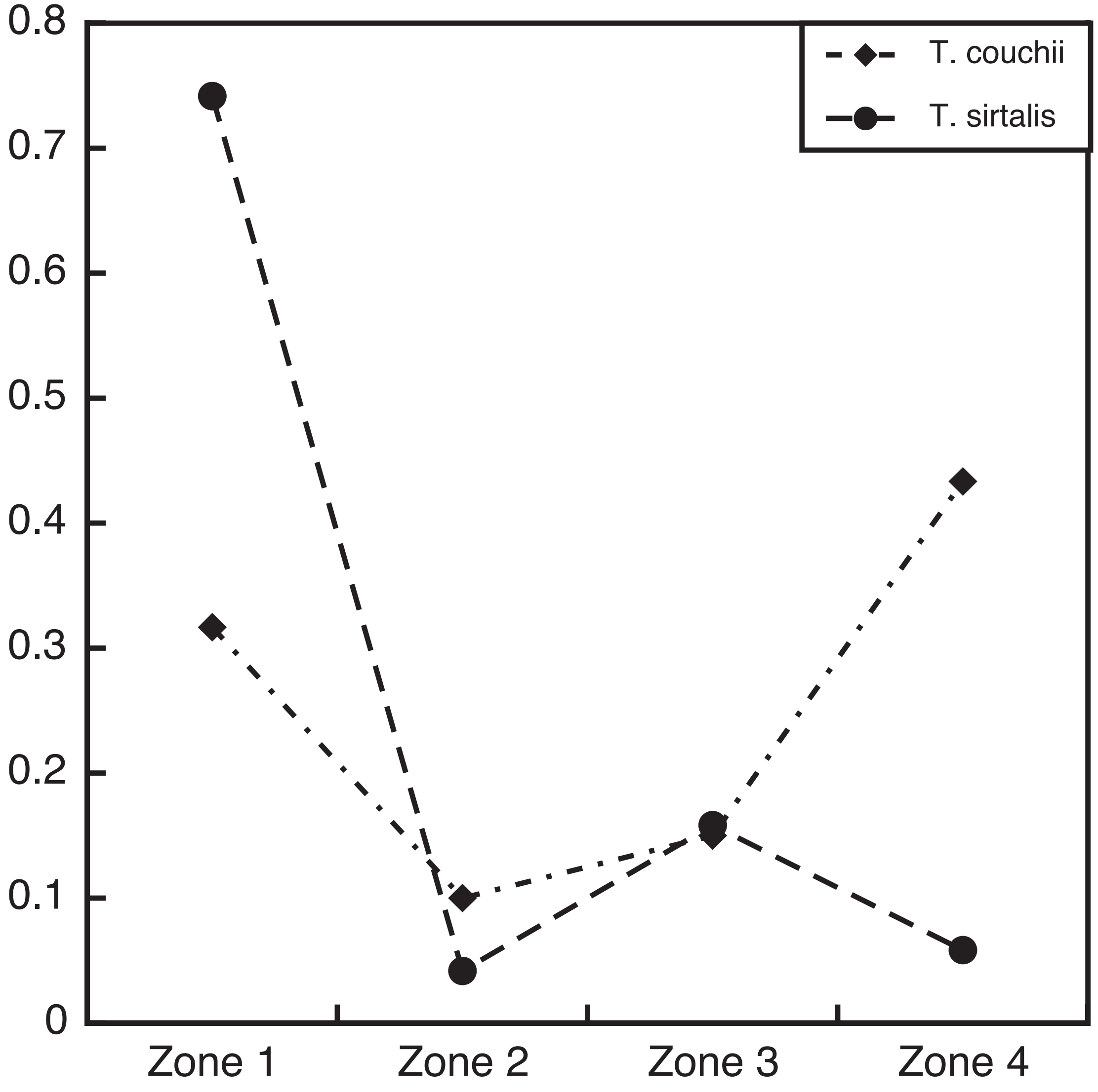

Fig. 8. Percentage of animals from each species in preferred zone from Lassen County when alone.

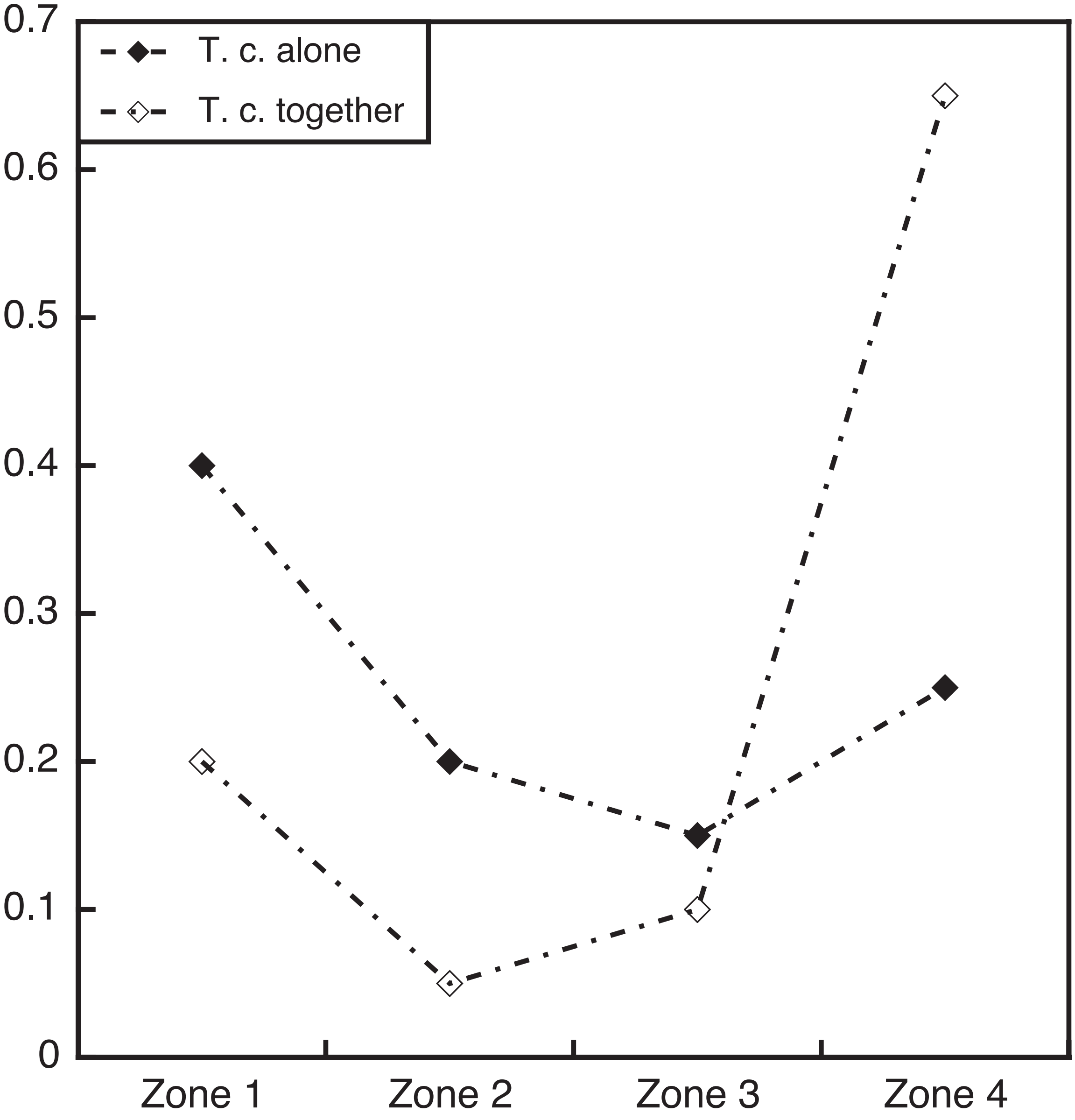

Fig. 9. Percentage of each species in preferred zone for *T. couchii* vs. *T. couchii* trial at Lassen County. *Thamnophis couchii* did not change habitat preference after addition of *T. couchii* (p> 0.05). *Thamnophis couchii* and *T. couchii* occupied similar zones when together (p<0.05). Preferred zone for *T.couchii* is the average number of snakes in each zone.

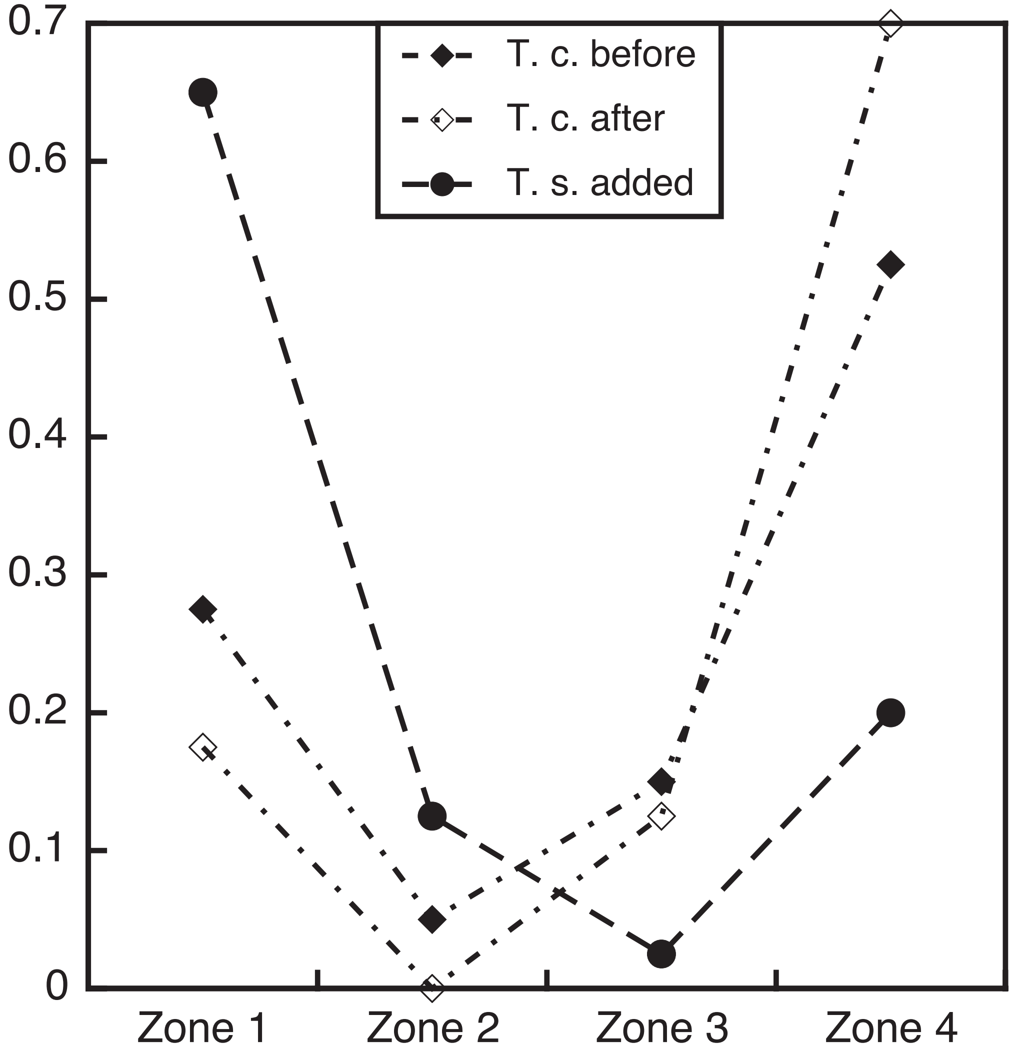

Fig. 10. Percentage of each species in preferred zone for *T. couchii* vs. *T. sirtalis* trial at Lassen County. *Thamnophis couchii* did not change habitat preference after addition of *T. sirtalis* ($p > 0.05$). *Thamnophis couchii* and *T. sirtalis* occupied different zones when together ($p < 0.01$).

The two *T. couchii* in the test chamber did not occupy significantly different zones (χ^2=4.692, p=0.2) (Fig. 9). No aggression between the two animals was observed. When *T. sirtalis* was added to the test chamber, *T. couchii* did not change its preferred zone (χ^2=1.99, p=0.58) (Fig. 10). *Thamnophis couchii* and *T. sirtalis* occupied different zones of the test chamber (χ^2=14.859, $p<0.01$) (Fig. 10). No aggression between the two animals was observed.

Thamnophis sirtalis

In every series of trials with a single *T. sirtalis* in the test chamber, they occupied zone 1 more than expected (22.25 of 30 snakes preferred zone 1) (Fig. 8). Introducing a second *T. sirtalis* to the test chamber did not cause the initial *T. sirtalis* to shift zones (χ^2=1.598, p=0.66) (Fig. 11). The two *T. sirtalis* in the test chamber did not occupy significantly different zones (χ^2=2.017, p=0.57) (Fig. 11). No aggression between the two animals was observed. When *T. couchii* was added to the test chamber, *T. sirtalis* shifted its location (χ^2=8.512, $p<0.05$) (Fig. 12). *Thamnophis sirtalis* and *T. couchii* occupied different zones of the test chamber (χ^2=22.744, $p<0.01$) (Fig. 12). No aggression between the two animals was observed.

Leoni Meadows (LM)

Thamnophis couchii

In every series of trials with a single *T. couchii* in the test chamber, they occupied zone 4 more often than expected (4 of 5 snakes preferred zone 4). When *T. sirtalis* was added to the test chamber, *T. couchii* did not change its preferred zone (3 of 5 snakes preferred zone 4). *Thamnophis couchii* and *T. sirtalis* did not occupy different zones of

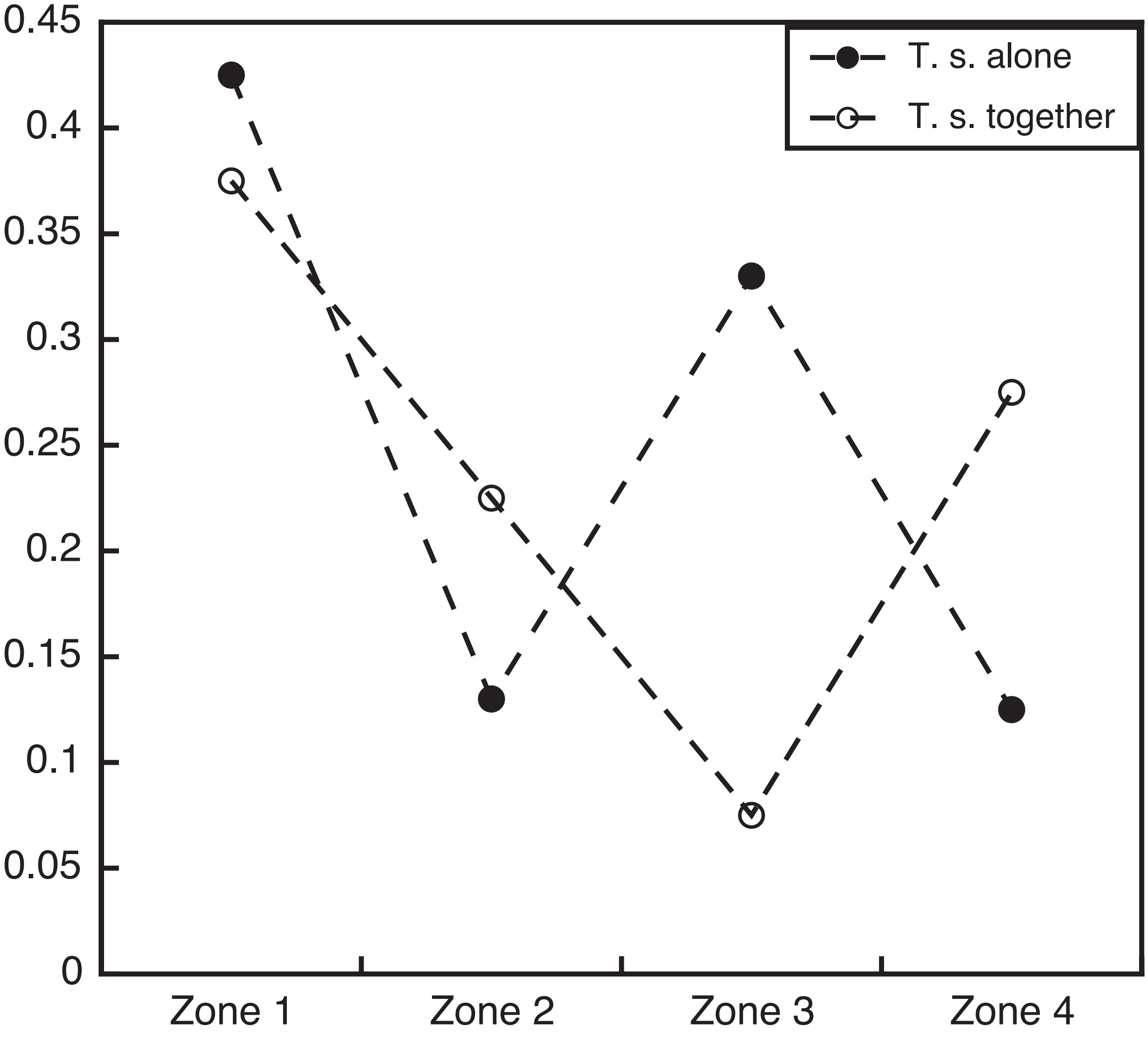

Fig. 11. Percentage of each species in preferred zone for *T. sirtalis* vs. *T. sirtalis* trial at Lassen County. *Thamnophis sirtalis* did not change habitat preference after addition of *T. sirtalis* ($p > 0.05$). *Thamnophis sirtalis* and *T. sirtalis* occupied similar zones when together ($p < 0.05$). Preferred zone for *T. sirtalis* is the average number of snakes in each zone.

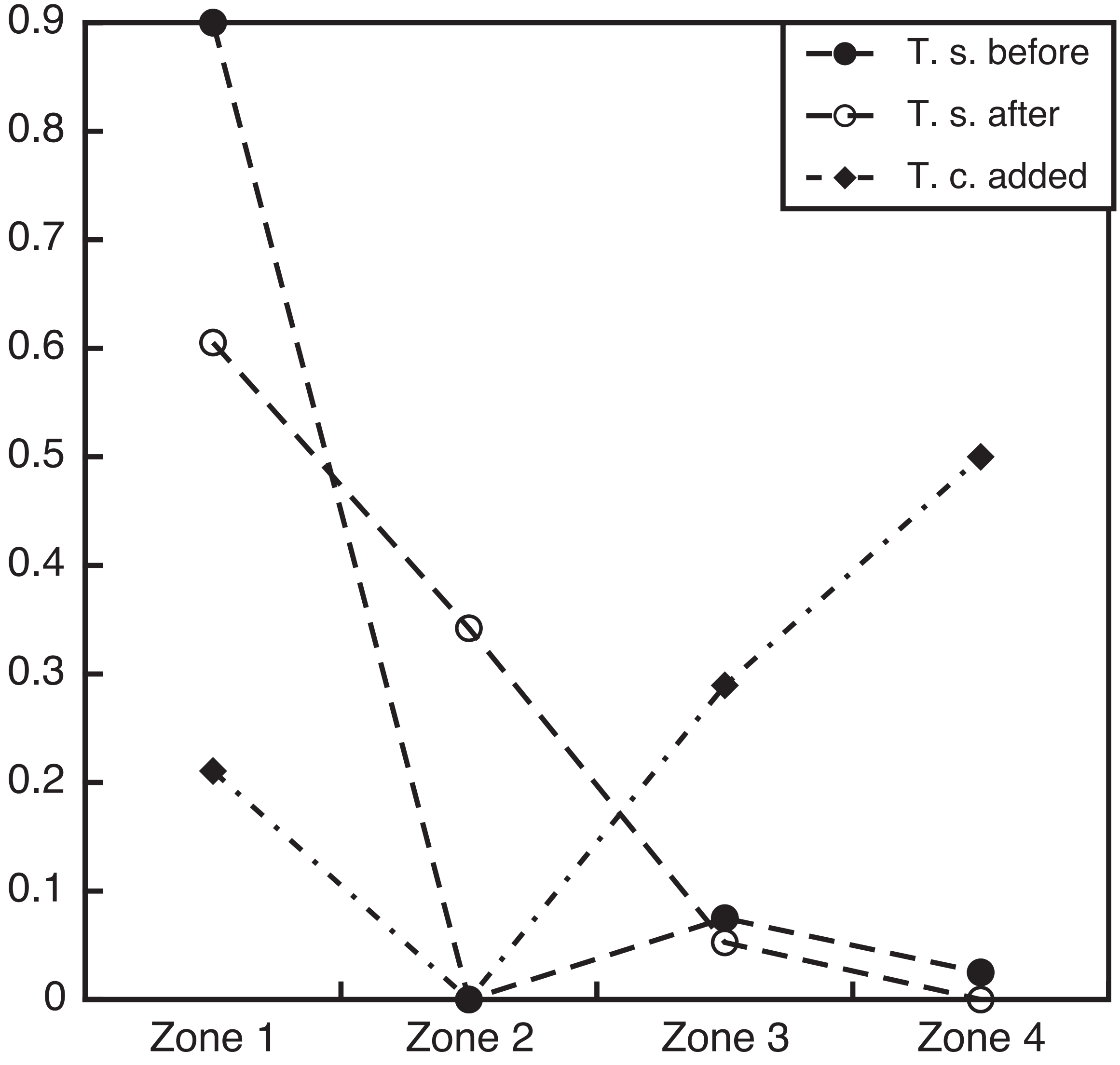

Fig. 12. Percentage of each species in preferred zone for *T. sirtalis* vs. *T. couchii* trial at Lassen County. *Thamnophis sirtalis* did not change habitat preference after addition of *T. couchii* ($p < 0.05$). *Thamnophis sirtalis* and *T. couchii* occupied different zones when together ($p<0.001$).

the test chamber (3 of 5 *T. couchii* and *T. sirtalis* preferred zone 4). No aggression between the two animals was observed.

Thamnophis elegans

In every series of trials with a single *T. elegans* in the test chamber, they occupied zone 4 more often than expected (5 of 5 snakes preferred zone 4). When *T. couchii* was added to the test chamber, *T. elegans* did not change its preferred zone (4 of 5 snakes preferred zone 4). *Thamnophis elegans* and *T. couchii* did not occupy different zones of the test chamber (4 of 5 *T. elegans* and 5 of 5 *T. couchii* preferred zone 4). No aggression between the two animals was observed.

Thamnophis sirtalis

In every series of trials with a single *T. sirtalis* in the test chamber, they occupied zone 4 more often than expected (5 of 5 snakes preferred zone 4). When *T. elegans* was added to the test chamber, *T. sirtalis* did not change its preferred zone (5 of 5 snakes preferred zone 4). *Thamnophis sirtalis* and *T. elegans* did not occupy different zones of the test chamber (5 of 5 *T. sirtalis* and 4 of 5 *T. elegans* preferred zone 4). No aggression between the two animals was observed.

Discussion

Most populations of garter snakes expressed preference for a particular zone. In most cases zonal preference varied both by population and species. The presence or absence of another snake sometimes affected the spatial use of the snakes.

Communication between animals is the “transfer of information from one individual to another.” Carpenter (1977), demonstrated that snakes are able to communicate. Mating and courtship communication was commonly observed between conspecifics. A small percentage displayed combat rituals, involving posturing and tactile pressure. Interspecific and intraspecific recognition plays an important role in mate choice, territoriality, and social level (Payne et al. 2004). Recognition has been demonstrated in salamanders, fish, ants, snakes, rodents, as well as in many predator prey systems (Wolff et al. 1983; Kleeberger 1984; Toft 1985; Hess and Losos 1991; Lancaster and Jaeger 1995; Brodman and Jaskula 2002; Smyers et al. 2002; Sullivan et al. 2002; Payne et al. 2004; Pinter-Wollman et al. 2006; Tsuruta and Goto 2007). We have observed unique combat rituals between *Thamnophis spp.* at SLP as well as differences between inter and intraspecific recognition and the consequences of this recognition on spatial preference.

Zonal preferences were expressed at all three populations of garter snakes. However, species from different populations expressed an affinity for different zones. The snake’s alone position for a 24-hour time period in the test chamber was considered it’s preferred space use. SLP snakes expressed a difference in zone preference by species. *Thamnophis atratus* (77%) and *T. elegans* (47%) showed a preference for zone 4 in all sets of trials. While *T. sirtalis* showed no particular affinity for any zone, spending approximately equal time in all four zones (Fig. 2). Lassen County snakes also expressed different zonal preferences by species. *Thamnophis couchii* expressed a preference for zone 4 (43%) and zone 1 (32%) while *T. sirtalis* expressed a preference for zone 1 (74%) (Fig. 8). LM snakes (>80%) all showed a strong affinity for zone 4.

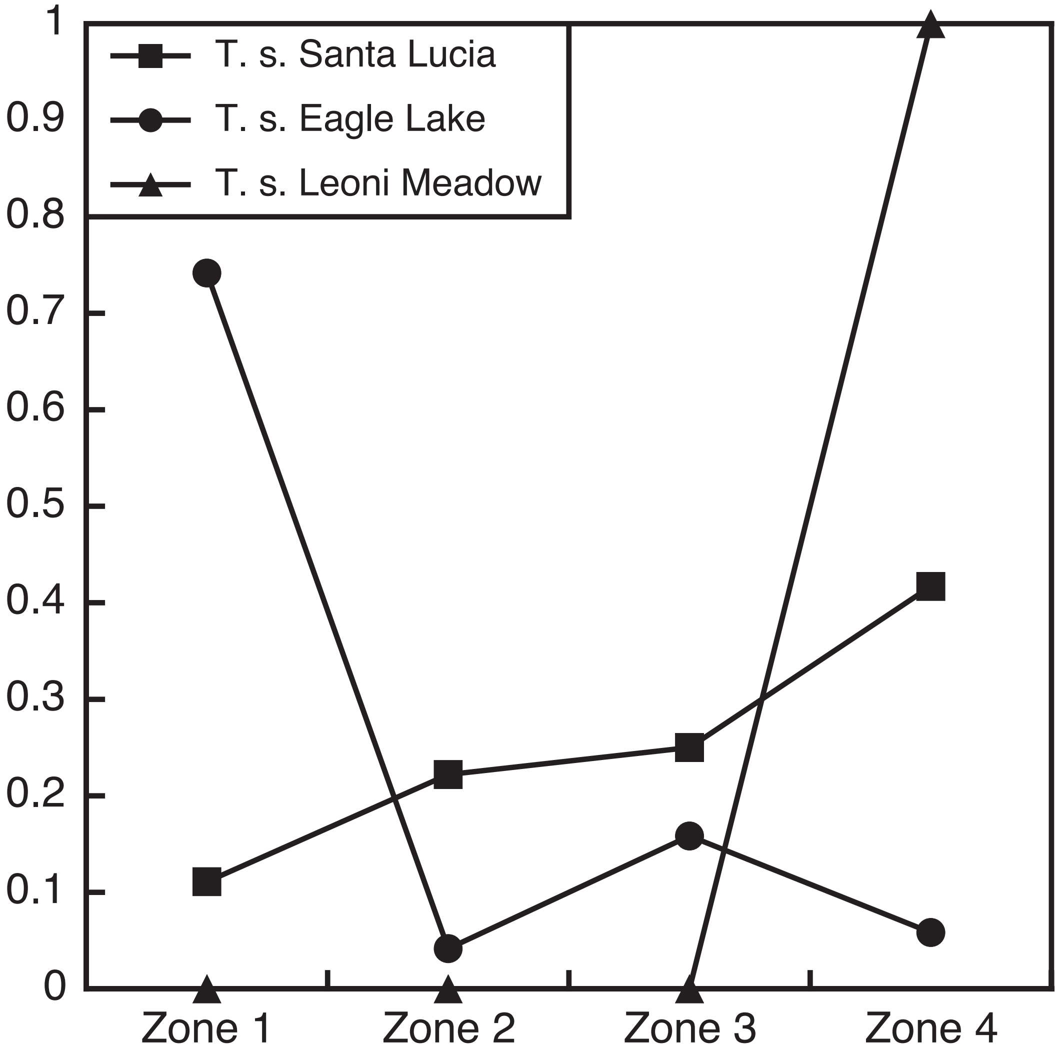

Fig. 13. Percentage of *T.sirtalis*, from each locality, in preferred zone when alone.

Thamnophis sirtalis populations at the different localities expressed different zonal preferences. SLP *T. sirtalis* spent approximately equal time in each of the 4 zones of the test chamber, showing no particular preference for any zone. Lassen County and LM *T. sirtalis* expressed different zone preferences from SLP and each other. *Thamnophis sirtalis* from LC expressed a strong affinity for zone 1 (74%), while *T. sirtalis* from LM was the opposite, preferring zone 4 (100%) (Fig. 13).

A pronounced shift in the preferred spatial occupation of *T. atratus* from SLP upon addition of *T. sirtalis* indicates that a unique behavioral interaction is occurring at SLP (Fig. 4). Occupying different zones from the predetermined preferred zone or maximizing the distance when in the presence of another snake would constitute a spatial occupation change; indicating the added snake as the superior snake. This trend did not occur between other species or at other localities (Figs. 3, 5, 6, 7, 9, 10, 12).

In most instances (21 of 24 snakes), *T. sirtalis* from SLP used direct behavioral interaction, including biting, aggressive displays, head and body flattening, hissing, and defense posture to induce a spatial occupation change in *T. atratus*. All of the strikes directed at *T. atratus* were directed toward the anterior quarter of the body. Changes in preferred spatial occupation may effect species distribution, species interactions, average animal size and abundance, as well as dietary trends and survivorship.

Thamnophis atratus from SLP altered their spatial occupation when in the presence of *T. sirtalis*. When the two species are alone they prefer zone 4 (Fig. 2). However, when together, *T. atratus* shifts it's spatial occupation, spending ~70% of the time removed from water, while *T. sirtalis* occupies zone 4 (~80%) (Fig. 4). This displacement, movement from preferred space, as determined by alone trials, to another space may be a result of similar biological and ecological needs. Interspecific territoriality is more likely to occur between biologically similar species (Hess and Losos 1991). Alone trials of *T. atratus* and *T. sirtalis* indicate that the species may have a similar biology and ecology. If both animals are vying for a limited resource (such as habitat or food) it is more likely that interspecific territoriality will occur (Reichenbach and Dalrymple 1980), possibly resulting in the spatial occupation shift that we have seen at SLP. Interspecific territoriality can present as aggression between two species. Twenty-one of 24 (87%) *T. sirtalis* demonstrated some level of aggression towards *T. atratus*. Further demonstrating that a possible interspecific territoriality may be occurring. Recently dispersing snakes have been shown to be more aggressive than snakes found in mating mode close to the den (Shine et al. 2003). This aggression however, was directed towards predatory simulation and not inter or intraspecific aggression. The snakes used in the SLP trials were either dispersing or had dispersed when captured. Putting them in possibly, their most aggressive behavioral condition.

Chemical signals may be responsible for aggression and segregation seen in other vertebrates, particularly between the common and spiny mouse (Pinter-Wollman et al. 2006). It is possible that the segregation and aggression that we have seen at SLP could be the result of chemical signals interacting between the two snakes. We, however, did not take this into account in our experimental design. Chemical interference, however, should be considered in future research.

Snake partitioning because of food is widely accepted (Reichenbach and Dalrymple 1980; Toft 1985). The spatial partitioning we have seen at SLP between *T. atratus* and *T. sirtalis* may be a direct result of food availability and choice. We have found, through examination of stomach contents, that the diets of *T. atratus* and *T. sirtalis* are not significantly different (p=0.09). The similarity of diets and preferred space use of *T. atratus* and *T. sirtalis* at SLP indicate that the snakes may have similar biologic needs. Spending at least some part of their time in the same habitat searching for and ingesting prey items. The displacement that we observed at SLP may be a direct result of territoriality and defense of a limited resource.

The addition of *T. atratus* to the test chamber had no effect on the position of *T. sirtalis* (Fig. 7). These data support that *T. sirtalis* is the dominant snake at SLP.

Through molecular analysis (mtDNA and nuDNA) (Feldman unpublished data) it was determined that SLP also had *T. elegans*. Separate trials were conducted to test *T. elegans* against both *T. atratus* and *T. sirtalis*. Examination of alone trials revealed that *T. elegans* preferred zone 3 and zone 4 (Fig. 2).

Trials between *T. elegans* and *T. atratus* showed no interspecific aggression or spatial occupation changes between the two species. However, only two trials of *T. atratus* vs. *T. elegans* were conducted, greatly reducing the power of the statistical analysis. Even with that in mind, no trend was evident between these two species.

Thamnophis elegans did show a spatial occupation change from when alone to when a *T. sirtalis* was added to the enclosure (χ^2=18.373, p<0.01). This change, however, was not to distance itself from the added snake, but rather to lessen the distance between the two species (Fig. 5). Contrary to experimental observations, during field observations *T. elegans* was located no closer than 50m to water. Stomach contents indicate that *T. elegans* at SLP eat primarily mammals. In addition, many *T. elegans* from SLP had bite marks and scars consistent with a diet of small mammals and a primarily terrestrial existence. Further investigation into the social interactions of *T. elegans* and *T. sirtalis* would help explain this unique experimental result.

In all of 55 trials with *T. sirtalis* at SLP aggression was seen in 43 of these (78%). The introduction of *T. sirtalis* to the chamber occupied by *T. atratus* resulted in aggression in 21 of 24 (88%) by the *T. sirtalis* over the course of the study. This aggression may help explain the spatial occupation shift that is detected in *T. atratus* upon addition of *T. sirtalis*. Eleven of 13 (85%) of *T. sirtalis* also displayed aggression towards *T. elegans* when added to a chamber occupied by *T. elegans*. Of the 10 trials involving *T. sirtalis* addition to a chamber occupied by *T. sirtalis* aggression was evident in 5 (50%) of these. The addition of *T. atratus* to a chamber occupied by *T. sirtalis* (8 trials) resulted in aggression from *T. sirtalis* in 100% of trials (8/8). Aggression was observed from *T. elegans* as well. Of the 13 trials involving addition of *T. sirtalis* to a chamber occupied by *T. elegans*, *T. elegans* was aggressive during 3 of these (23%). No aggression was recorded from *T. atratus*.

During collection, it was evident, that *T. atratus* were spending time in different areas at allopatric and sympatric ponds. Pond 234, a *T. atratus* only pond, 100% of the snakes were no more than 1 meter from the water, with >90% of the snakes captured in the water. This pond was repeatedly collected from water’s edge to 20 meters from water; 100% of the collected animals were found within 1 meter of the water. The animals at this pond were consistently small, with average snout vent length (SVL) 42.5 cm; this small size was true for animals throughout the SLP. It is possible that the small size of *T. atratus* at SLP is a result of two different mechanisms directly related to *T. atratus* being forced to occupy a suboptimal habitat because of *T. sirtalis*. Allopatric pond snakes have a lot of biomass in a small area. This may make food the limiting resource for these snakes and make *T. atratus* allopatric ponds in some way less productive than sympatric ponds. This theory remains to be tested. A second mechanism at work may be exclusion from prime feeding habitat at sympatric ponds. We demonstrated that *T. sirtalis* forces *T. atratus* to occupy a sub optimal space as determined by observation and experimental trials, this has also been observed in other animals. Ambystomatid salamanders have been shown to vacate their preferred habitat soon after a behavior altercation with a superior species, creating a “fugitive species,” forcing the inferior competitor to relocate (Smyers et. al. 2002). *Thamnophis atratus* may be forced to be the “fugitive species” at the SLP, vacating a preferred habitat after one altercation, forced to utilize different food resources or find another area where an altercation will not occur.

The other spectrum was pond D-19/21, a sympatric pond that had both *T. sirtalis* and *T. atratus*. *Thamnophis sirtalis* were collected between 1 and 20m from the waters edge. *Thamnophis atratus*, however, was collected up to 50 meters from the water at this locality. *Thamnophis atratus* was less prevalent at Wetlands and Morse, other sympatric collection sites, than at pond 234. Low *T. atratus* numbers at sympatric sites such as D-19/21, Morse, and Wetlands may be a result of *T. atratus* not being in its preferred habitat. Possibly the result of *T. sirtalis* forcing *T. atratus* from water, where it typically seeks food and refuge from predators (Stebbins 2003) which may increase the predation rate and overall mortality on the species at sympatric ponds.

Summer months at SLP bring many ecological changes, including drying of grasslands and greatly reduced water levels. The changes that occur throughout the summer greatly reduce the suitable habitat and resources for *Thamnophis spp.* Wolff et al. (1983) hypothesized that if two species are similar enough and persist in a homogeneous environment with limited but definable resources they should exhibit interspecific territoriality. This hypothesis may be applicable to the interactions observed at SLP. During the summer, resources (water and food) for *T. atratus* and *T. sirtalis* are declining at a rapid rate, forcing the animals to occupy a more compact space; resulting in a behavior that has not been seen at other locales.

Two other localities were tested and showed no significant change in spatial occupation by any species of snake, placing further emphasis on the unique findings at SLP. Leoni Meadows trials showed no significant difference in spatial occupation of snake species. Collection numbers were low at LM because of difficult collecting. Sampling efforts were not extended at LM because the data that were collected did not show any behavior or spatial occupation trends. Although low numbers affected statistical power, the trials conducted showed no support for the data at SLP.

Thamnophis sirtalis and *T. couchii* at LC occupied different habitats when alone and had no effect on each other when together (Figs. 8, 10, 12). Diets of *T. sirtalis* and *T. couchii* from LC were also examined. Stomach contents differed significantly between *T. sirtalis* and *T. couchii* ($p<0.01$). Differences in diet may indicate that the snakes have different biologic and ecologic needs and interspecific aggression will be unlikely. The addition of *T. sirtalis* to the test chamber occupied by *T. couchii* did not change the spatial occupation of *T. couchii* (Fig. 10). Likewise, the addition of *T. couchii* to the test chamber occupied by *T. sirtalis* did not change the spatial occupation of *T. sirtalis* (Fig. 12). The lack of interactions between these two species and the lack of overlap of diet further supports the possibility that interactions may only be seen in biologic and ecologic similar species such as those found at SLP.

CHAPTER 3

DIET HABITS OF *THAMNOPHIS*

Introduction

An organism’s diet not only provides insight to its feeding habits, but also gives a glimpse to the many ecological, biological, and evolutionary interactions that may be occurring. Diet studies are the cornerstone of ecological research. Diet data provides information on the preferred habitat of an organism, answers questions about an animals growth and resource utilization, and lays the groundwork for questions about competition of closely related species and possible evolution of prey defenses and predator response to those defenses.

Much research has been devoted to snake diet, in particular *Thamnophis* and *Nerodia* (Arnold, Gregory, Mushinsky, and others). Many of these studies involve collecting snakes at a single locality, in a single year, often times in a single season, and reporting the diet based on this data. Other studies, however, argue that snake diets fluctuate throughout years and change according to the rules of the optimal foraging theory (Pyke et al. 1977; Kephart and Arnold 1982; Garcia and Drummond 1988). These studies caution that a single year diet study may not accurately reflect the diet of the animal. Cautioning that season, temperature, and prey base may alter the primary food consumed by snakes throughout the year. A more recent trend in snake foraging ecology research is to describe the relationship between snake size and prey size (Mushinsky et al. 1982; Garcia and Drummond 1988; King 1993; Greene et al. 1994; Gregory and Isaac 2004), even so far as to describe orientation of prey ingestion (Cobb 2004). Studies that link prey size to snake size may be trying to bridge the gap. Still yet, much research focuses on the relationship between diet and habitat (Hyslop 1980; Mushinsky et al. 1982; Drummond and Burghardt 1983; Garcia and Drummond 1988; Arnold 1992). Such a relationship is readily examined within a single species. However, when multiple species diets and habitats are examined, the relationship may not be so evident, especially when the species vie for similar prey.

The Santa Lucia Preserve (SLP) is a 35 square mile preserve located in the Santa Lucia Mountains in Monterey Co. California. The uniqueness of the preserve is evident as several different ecosystems are located within its boundaries, arboreal forest, pine forest, grassland, wetland, and aquatic. The diverse ecosystems at SLP serve as habitat for several different *Thamnophis* species as well as many different potential prey items, including the toxic *Taricha torosa*. The close proximity of these diverse habitats facilitates many inter-generic and inter-specific interactions. The potential toxic prey items, diverse habitat, and abundant snake populations make SLP an ideal location for this diet study.

Thamnophis sirtalis, T. atratus, and *T. elegans* are three species whose diet has been well studied the past several decades (Fitch 1965; Fouquette 1954; Carpenter 1952; White and Kolb 1974; Arnold and Wassersug 1978; Gregory et al. 1980; Kephart and Arnold 1982; Drummond and Burghardt 1983; Arnold 1992). Ongoing diet data collection by Steve Arnold and others have made it possible to compare historical diet trends with current diet data. As well as compare statewide diet data with that of a more localized area. The diverse collection localities visited by Arnold and others and the data from SLP make it possible to determine how frequently *Thamnophis* species utilize different prey, including the toxic amphibian *Taricha torosa*. Finally, comparison of historical statewide diet data with data from SLP may shed light onto the relatedness of several of the species diets.

Methods

Santa Lucia Preserve

Snakes were collected by hand throughout SLP between 05 May 2004 and 27 September 2006. Upon capture, each animal was SVL measured, weighed, given a unique ventral scale clip for future identification, and forced to regurgitate (Carpenter 1952). Animals were then released at the site of capture.

Each food item was identified and classified as one of seven categories; anuran, leech, slug, salamander, mammal, fish, and other. A chi-square test for homogeneity was then performed on the three species of snakes from SLP to test for diet differences. Percentages of each category of food were also determined for each species of snake.

Arnold

Diet data obtained from stomach contents from 1972 through 2006 was analyzed using the same method as SLP. Only collection localities that coincide with the California geographic range of toxic *Taricha* were analyzed. This included five species of snakes (*T. atratus, T. sirtalis, T. elegans*, *T. couchii,* and *T. ordinoides*) from 20 different localities. The diet data of *T. elegans, T. atratus,* and *T. sirtalis* was analyzed with the other two species and by itself for comparative purposes.

Comparison

Thamnophis atratus, T. elegans, and *T. sirtalis* diet data from SLP and from Arnold's data set were compared. A chi-square test for homogeneity was performed on the groups as a whole and on each species separately to test differences in diet.

Results

In total, 222 snakes were collected at Santa Lucia Preserve. I collected 179 stomach contents from 94 snakes at Santa Lucia Preserve from 2004 to 2006. I also analyzed 2948 food items identified by Steven Arnold and others from 1070 snakes collected by Steve Arnold and others from 1972 to 2006. A total of 3979 snakes was collected by Steve Arnold and others. The two data sets will be discussed separately and then compared. Prey has been classified into seven major categories, anuran, fish, leech, slug, salamanders, mammals, and other/unidentified.

Santa Lucia Preserve

Thamnophis elegans, T. atratus, and *T. sirtalis* were collected from the SLP and forced to regurgitate. In total, 179 prey items were collected from 94 snakes of 222 captured (43% of total number captured) (Table A2). *Thamnophis elegans* had the smallest range of food items, ingesting only two of seven categories of food, mammal and unidentified. *Thamnophis atratus* had five different categories of food items in their stomachs including anuran, leech, slug, salamander, and unidentified. *Thamnophis sirtalis* had three of seven food categories in their stomach including anuran, salamander/lizard, and unidentified (Fig. 14).

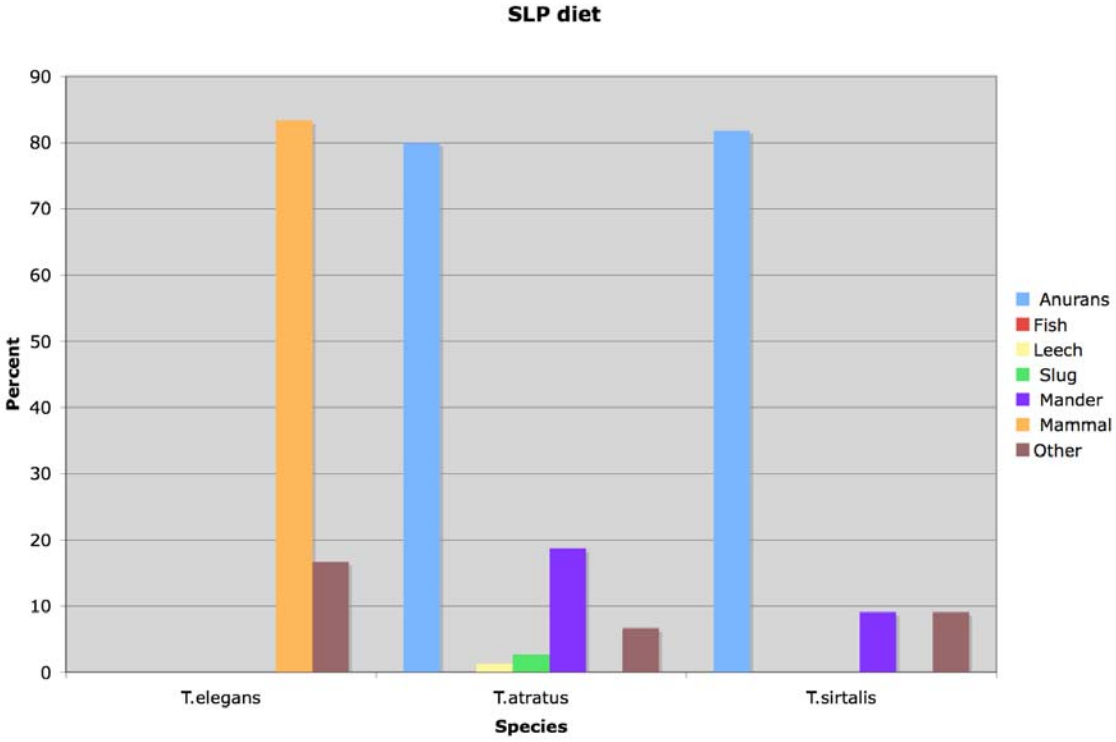

Fig. 14. Percentage of prey in the stomachs of *T. elegans*, *T. atratus,* and *T. sirtalis* at the Santa Lucia Preserve from 2004 to 2006. The diets of the snakes varied significantly based on the number of stomachs ($p=5.2x10^{-14}$).

Diets of *T. elegans, T. atratus,* and *T. sirtalis* varied significantly ($p<0.01$). Diets of *T. atratus* and *T. sirtalis* were compared separately and do not vary significantly ($p=0.90$).

Food items appear correlate to the habitat where the snakes where captured. *T. elegans* were found primarily under cover objects in large fields 50 or more meters from water. Most of the food items recovered (83%) from *T. elegans* were mammals. The majority *T. atratus* were captured within 1 meter of the edge of a pond. The food items found in *T. atratus* stomachs included anurans, leeches, slugs, salamanders, and several unidentified. *Thamnophis sirtalis* were found within 20 meters of pond edges, food items include anurans, salamanders, and an unidentified (Fig. 14). These data reflect that the habitat that the snake occupies has an effect on which types of food are found in the snake.

Taricha torosa has been found in the stomachs of *T. sirtalis* and *T. atratus* during this diet study at SLP. An adult *T. torosa* was recovered from the stomach of an adult *T. sirtalis* at SLP. Juvenile *T. torosa* were recovered in the stomachs of *T. atratus* at SLP.

Arnold

Thamnophis atratus, T. couchii, T. elegans, T. ordinoides, and *T. sirtalis* were collected from 20 localities (Appendix B, Figs. B1-B18) from within the California range of toxic *Taricha torosa.* In total, 2948 food items were recovered from 1070 of the 3979 snakes (27% of total snakes captured) between 1972 and 2006 by Steven Arnold and others.

Diets of the five snake species varied significantly ($p<0.01$) (Fig. B15). *Thamnophis elegans* had the broadest range of food items, consuming prey in each of seven categories (Table A3). *Thamnophis atratus* had the smallest range of food items, consuming only anurans, fish, and salamanders.

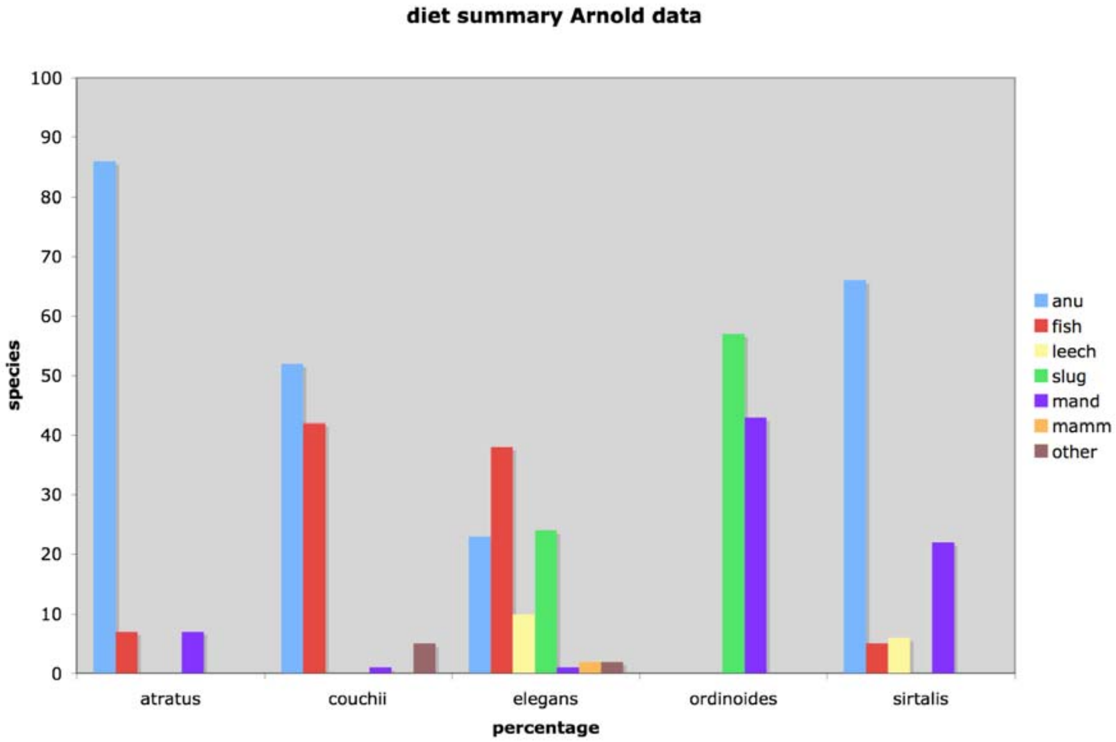

Fig. 15. Percentage of prey in the stomachs of *T. atratus, T. couchii, T. elegans, T. ordinoides,* and *T. sirtalis* from historical data. The diets of the snakes varied significantly based on the number of stomachs ($p=4.9x10^{-59}$).

The diets of *T. elegans, T. atratus,* and *T. sirtalis* were analyzed as a group using chi-square. Diets of *T. elegans, T. atratus,* and *T. sirtalis* varied significantly (p<0.01). However, the diets of *T. atratus* and *T. sirtalis* did not vary significantly based on the overall number of stomachs (p=0.13).

Taricha torosa was found in the stomach of one *T. sirtalis*, Clark/Clarktown locale, and one *T. atratus*, Mocho locale. Finding *Taricha* as prey items in *T. atratus* at Mocho demonstrates that *T. atratus* will utilize *Taricha* as a prey item throughout their range.

Comparison

Diets of *T. atratus, T. sirtalis,* and *T. elegans* from SLP collected between 2004 and 2006 were compared to the diets of *T. atratus, T. sirtalis,* and *T. elegans* collected by Steve Arnold and others between 1972 and 2006 in localities of California range overlap with toxic *Taricha torosa*. The analysis revealed several diet and population trends.

Diets of *T. atratus, T. sirtalis,* and *T. elegans* were compared between the two data sets at the species level (Fig. 16). *Thamnophis atratus* diets did not differ significantly ($p=0.06$). Although *T. atratus* from Arnold's data and from the SLP consume anurans as their main food source, *T. atratus* from SLP have a much broader diet range ingesting prey from five of seven prey categories. *Thamnophis atratus* collected by Arnold and others contained prey from three of seven categories. *Thamnophis atratus* utilized salamanders as a major item in their diet (19%) whereas *T. atratus* collected by Arnold and others very seldom use salamanders as a food source (7%).

Thamnophis sirtalis diets from the two data sets differ significantly ($p<0.05$). *Thamnophis sirtalis* from both data sets utilize anurans as their primary food source (SLP 69%, Arnold 70%). Salamanders were the next most abundant item (SLP 15%, Arnold 23%) in the diets of *T. sirtalis*.

Thamnophis elegans diets differed significantly between the two data sets ($p<0.01$). The diet of *T. elegans* from SLP consisted only of mammals and one unidentified stomach content. The diet of *T. elegans* from Arnold's data, however, consisted of items from all 7 categories of food with fish being the primary food item found in the stomachs (38%).

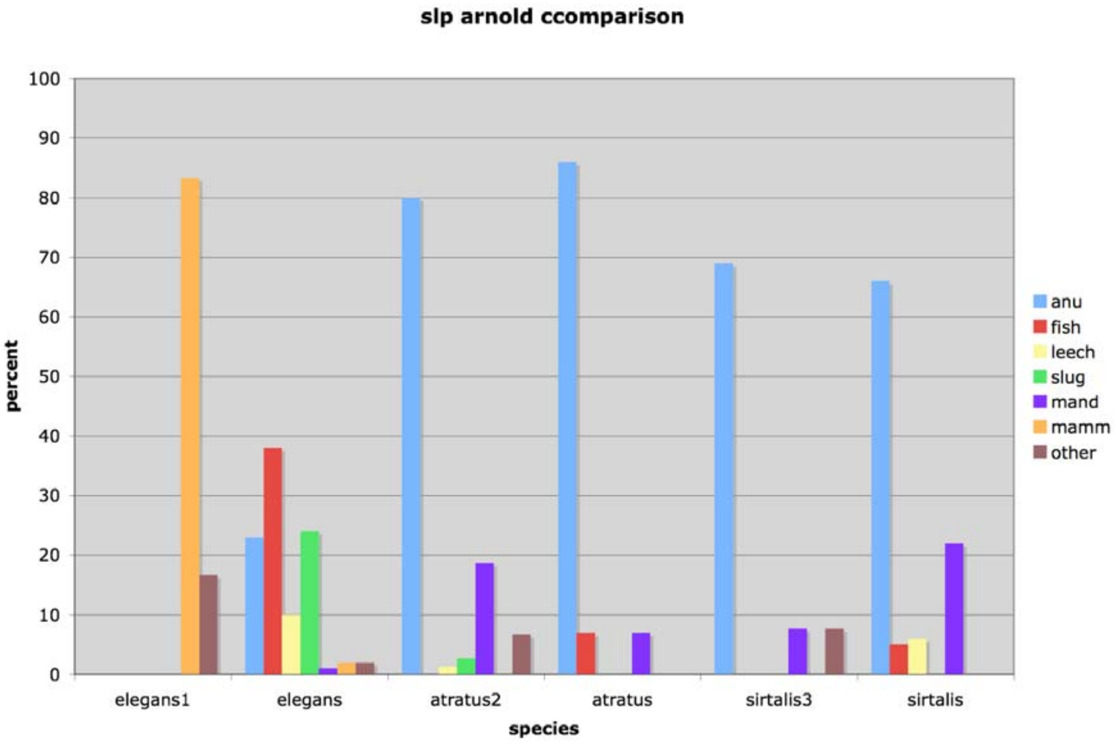

Fig. 16. Comparison of the percentage of prey in the stomachs of *T. elegans, T. atratus,* and *T. sirtalis,* from SLP (numbered) and historical data. *Thamnophis elegans* diet varied significantly based on the number of stomachs ($p=43.36x10^{-30}$). *Thamnophis atratus* diet did not vary significantly based on the number of stomachs (p=0.064,). *Thamnophis sirtalis* diet varied based on the number of stomachs (p=0.025).

The items found in the stomachs of *T. atratus* and *T. sirtalis* from SLP appear to be correlated to the size of the snake. A total of 60 *T. atratus* stomachs had anurans. The anuran items found in the stomachs of *T. atratus* were mainly larval, recently metamorphosed, or juveniles consistent with the diet of a smaller gape limited snake. A total of nine *T. sirtalis* had anurans. The anuran items found in *T. sirtalis* stomachs, however, were either juvenile or adult, there were no larval anurans found in the stomachs of *T. sirtalis*, consistent with a predator whose anuran diet is not limited by its size.

Diet of *T. atratus* and *T. sirtalis* from Arnold's data does not have the same trends as the diet data from SLP. *Thamnophis sirtalis* from Arnold's data utilizes salamanders as a much larger part of their diet than do *T. sirtalis* from SLP, where they mainly utilize anurans. *Thamnophis atratus* from Arnold's data utilizes anurans as the primary food with only the occasional other food item. SLP *T. atratus* also primarily utilize anurans but also ingest salamanders as a secondary food source.

Discussion

Santa Lucia Preserve

Forty-four percent of snakes captured at SLP contained food items. This is slightly higher than the 30% average found in most diet studies (Gregory and Isaac 2004). The diets of *T. elegans, T. atratus,* and *T. sirtalis* at SLP vary significantly and appear to correlate with the habitat where the snake was found.

Previous studies have shown *T. elegans* to feed primarily on aquatic organisms, including fish, anurans, and leeches (Arnold 1981, 1992; Kephart and Arnold 1982; Drummond and Burghardt 1983). Kephart and Arnold (1982) reported that the diet of *T. elegans* was highly variable among years and the most abundant food item was the most abundant prey during the given season of the given year. Although variable, they found primarily anurans, fish, and leeches as stomach contents, and also reported that *T. elegans* would shift their optimal foraging site in relation to prey base. Drummond and Burghardt (1983) reported that differences exist in *T. elegans* diet based upon habitat. They found that coastal *T. elegans* fed primarily on slugs with the occasional mammal, anuran, lizard and salamander. While inland *T. elegans* had a diet similar to that found by Kephart and Arnold (1982), existing primarily on anurans, fish, and leeches, with the occasional mammal and lizard. Yet other studies have reported different food items for *T. elegans*, including a diet of primarily fish and birds (White and Kolb 1974). Fleharty (1967), has reported that *T. elegans* has "generalized feeding habits," noting that half of the stomachs he examined contained aquatic food items and the approximately half consisted of terrestrial food items of animals found "near aquatic environments." Still yet, other studies report *T. elegans* preference and handling ability for mammals and other difficult to handle prey, including toxic prey (Gregory et al. 1980; Arnold 1992). Amongst the differences found in the literature on *T. elegans* food habits, one underlying principle remained consistent, *T. elegans* consumed the most profitable prey available at the given time and that food choice may correlate with habitat.

Thamnophis elegans from SLP, contrary to many of the aforementioned studies, appear to specialize on terrestrial organisms, mainly mammals (83%). Several studies have demonstrated diet and habitat to be correlated (Drummond and Burghardt 1983; Garcia and Drummond 1988; Arnold 1992; King 1993; Greene et al. 1994; Gregory and Isaac 2004; Lind et al. 2005). Although not directly tested at SLP, a relationship between diet and habitat seems to exist. *Thamnophis elegans* were captured in dry fields at least 50 meters from water and stomach contents only contained small mammals, possibly demonstrating a diet and habitat correlation.

The narrow scope of *T. elegans* diet at SLP disagrees with previous studies conducted on *T. elegans*. Previous studies have shown *T. elegans* to be a generalist predator and consume the most profitable prey available (Fleharty 1967; White and Kolb 1974; Kephart and Arnold 1982; Drummond and Burghardt 1983). My results, however, indicate that *T. elegans* at SLP are specialized towards small mammals. Snakes that did not contain food items had numerous bite marks and scars consistent with previous studies and with interactions with small mammals (Gregory et al. 1980).

Thamnophis atratus had the widest range of prey items including anurans (80%), leeches (1%), slugs (3%), salamanders (19%), and some unidentified items (7%). Anurans were plentiful throughout the year in and at the edges of ponds; all of the *T. atratus* collected for this study were captured within one meter of the pond edge, possibly showing a habitat and diet relationship. Salamanders were the next most prolific item in *T. atratus* stomachs. Although not tested, a dietary shift appeared to occur as prey base shifted. Salamander larvae became more abundant in the aquatic system as the air temperature increased. Subsequently, as has been found in other studies and supported by optimal foraging theory (Pyke et al 1977; Kephart and Arnold 1982), as this food item became more available, *T. atratus* ingested it more.

The majority of *T. atratus* (78%) captured for this study were concentrated around one pond where *T. sirtalis* and *T. elegans* were not found. The average size of *T. atratus* from this pond is smaller than the average *T. atratus* that were captured elsewhere at SLP. The smaller size of *T. atratus* at this locality (average size 42.9 cm pond 234, average size 46.9 cm other) may be attributed to the large number of *T. atratus* in a small area. Pond 234, however, also contains a large prey base of salamanders and anurans, from larval to adult stages, providing food for all size classes of *T. atratus* at this locality.

More research is needed to determine if there is a correlation between *T. atratus* size at this locality, population numbers, and prey base.

Thamnophis sirtalis diet was consistent with the diet of *T. atratus* from SLP (p=0.08); anurans constituted 82% of *T. sirtalis* diet. Kephart and Arnold (1982) reported that the primary prey consumed by *T. sirtalis* throughout a 7-year study was anurans and *T. sirtalis* was unable to switch to alternative prey resources when anurans were not particularly abundant. Arnold (1992) also commented that *T. sirtalis* has an affinity for anurans but will consume annelids as an alternative prey. He also noted that there is a level of preference for fish, as demonstrated by behavior. Fitch (1941a, b), and White and Kolb (1974) also demonstrated that *T. sirtalis* has an affinity for anurans. Anurans have been shown to constitute as much as 55.5% of *T. sirtalis* diet (White and Kolb 1974).

All *T. sirtalis* were collected within 20 meters of water showing that a habitat and diet relationship may also be occurring with *T. sirtalis*, as previously mentioned (Drummond and Burghardt 1983; Garcia and Drummond 1988; Arnold 1992; King 1993; Greene et al 1994; Gregory and Isaac 2004; Lind et al. 2005). The overall number of *T. sirtalis* (44 total animals) was lower than the number of *T. atratus* (150 total animals) used in this study. Kephart and Arnold (1982) found similar trends for the seeming relative rarity of *T. sirtalis* during their 7-year study of sympatric *Thamnophis* species (*T. elegans* 493: *T. sirtalis* 36). Several possible explanations exist for this finding at SLP. *Thamnophis sirtalis* were much more difficult to locate, being captured within a 20-meter vicinity of water, whereas *T. atratus* were found within 1 meter of water. *Thamnophis sirtalis* utilized small mammal burrows and other holes in the ground for cover, escape, and overnight, making capture much more difficult. Finally, the water areas that *T. sirtalis* occupied where heavily inundated with vegetation, making sighting and capture extremely difficult. *Thamnophis sirtalis* (average size 67.9 cm) from the SLP were larger than *T. atratus* (average size 43.8 cm); and were not concentrated at any specific area. The low numbers of *T. sirtalis* at SLP may be facilitating larger snakes. A single snake may be able to actively forage over a larger area because of fewer competitors, and utilize a larger percentage of the available resources. This hypothesis, however, is yet to be tested and will benefit from future research at SLP.

Arnold

Of the five snake species collected by Steve Arnold and others that overlap with the California range of the toxic *Taricha*, 28% contained food items. This number is consistent with previous studies of snake diets that average 20-30% of snakes with food in their stomachs (Gregory and Isaac 2004). The diets of *T. atratus, T. elegans,* and *T. sirtalis* are of particular interest for comparative purposes.

Thamnophis elegans is the most general predator of the three, consuming prey items in all seven categories. Indicating that *T. elegans* does not have a prey preference and will consume the most profitable prey. This finding is consistent with previous studies that report *T. elegans* will switch it feeding habits to the prey that is most profitable at the any given time (Fleharty 1967; White and Kolb 1974; Kephart and Arnold 1982; Drummond and Burghardt 1983; Arnold 1992). *Thamnophis atratus* and *T. sirtalis*, however, consume a large percentage of anuran prey relative to other prey categories (*T. atratus*=89%, *T. sirtalis*=70%). Little information exists on the diet of *T.*

atratus. However, the findings of *T. sirtalis* from the historical data are consistent with the large body of data that describes *T. sirtalis* as primarily feeding on amphibians (Fitch 1941a, b; White and Kolb 1974; Kephart and Arnold 1982; Arnold 1992).

The collection localities of *T. atratus* and *T. sirtalis* provide insight to the diet and possible interactions of these two species. Although I am unable to determine the microhabitat where each snake was collected, general locality is known. There is little overlap in collection locality for *T. atratus* and *T. sirtalis*. Only one locality had both species, Mocho, and the collection numbers are heavily skewed towards *T. atratus* (*T. atratus*=64, *T. sirtalis*=4). The differences in collection locality allow speculation on relatedness of the diet between *T. sirtalis* and *T. atratus* (p=0.23). The lack of a competing species for potential prey items may foster the growth and reproduction of the species that is present. This hypothesis, however, remains to be tested.

Thamnophis elegans is commonly found at the localities where *T. atratus* and *T. sirtalis* are collected. The ability of *T. elegans* to consume a large number of different prey items may allow the sympatric existence of these species (Arnold 1981; Kephart and Arnold 1982; Drummond and Burghardt 1983; Arnold 1992). Lack of competition for prey items may allow the different species to coexist. It is unclear though, whether the sympatric existence has fostered the generalized diet or the generalized diet fostered the sympatric existence. This is an interesting quandary that will benefit from future research.

Comparison

Similar trends in the diets of *T. atratus, T. elegans*, and *T. sirtalis* between the SLP and Arnold's historical data are apparent. The diet of each species was compared. The diets of *T. elegans* and *T. atratus* from the two data sets differed significantly (p<0.01 and p=0.06). The large difference seen between *T. elegans* diets may be attributed to habitat difference. *Thamnophis elegans* at SLP was only found in open fields at least 50 meters from water and only contained small mammals. *Thamnophis elegans* from Arnold's data, however, has a varied diet, possibly indicating that *T. elegans* is found in a variety of habitats throughout California and is not generally restricted to a certain habitat. Both scenarios may foster coexistence with *T. atratus* and *T. sirtalis* at the given localities.

Thamnophis atratus from SLP and Arnold's data both consumed primarily anurans, but SLP *T. atratus* had a broader range of food items. *Thamnophis atratus* from SLP utilized salamanders twice as often as *T. atratus* from Arnold's data (>19%: <9%). The difference in salamander consumption may be a reflection of the locality or other physiologic factors. *Thamnophis atratus* from SLP may be more adept at consuming salamanders, *Taricha torosa* specifically, and are able to include them as major dietary item. On the other hand, *T. atratus* from other California locales may not be able to process the noxious secretions of salamanders as efficiently and do not ingest them as often. This hypothesis waits testing.

Thamnophis sirtalis diets from the two data sets differ significantly (p<0.05). *Thamnophis sirtalis* from SLP and throughout California utilize anurans as their primary prey source (69%) with the occasional salamander (15%). The similarities of *T. sirtalis* and *T. atratus* diet at SLP and in a broader geographic area provide information on the lack of local sympatry that is seen with these two species. Possible competition for common food items may be inhibiting coexistence.

The lack of sympatry between *T. atratus* and *T. sirtalis* in both data sets may indicate that these two species of snake are avoiding each other. It is clear that the two species prey on similar items (SLP p=0.90, Arnold p=0.13), which may force them to compete for common food items when found in sympatry. This competition may lead to local extinction or force one species to find a locality not yet occupied by the other (Reichenbach and Dalrymple 1980; Griffis and Jaeger 1998; Olson and Warner 2001; Smyers et al. 2002; Luiselli 2006). The narrow diet of *T. elegans* at SLP excludes it from possible competition for food with *T. atratus* or *T. sirtalis*. The diet of *T. elegans* from Arnold's data also excludes it form possible competition for food with *T. atratus* and *T. sirtalis* and subsequently has been found at the same localities. The possible competition and interaction between different snake species based on diet is an interesting idea that will benefit from future research.

CHAPTER 4

CONCLUSION

Animal interactions are common in the natural world and often lead to unique natural histories. I observed several species of *Thamnophis* at SLP that were interacting, or not interacting, in a way that may affect their biology. Examining the interspecific interactions of *T. sirtalis, T. atratus*, and *T. elegans* at SLP provided insight into the different biologies that I have observed in these snakes at this locality. I also tested interspecifc and intraspecific interaction between similar *Thamnophis* species at several localities throughout California to determine if the behavior observed SLP was unique. The second aspect of my study was a broad range diet study of several *Thamnophis* species throughout the state of California in regions of overlap with their toxic prey *Taricha spp.* The data that were collected compliment the behavior study, provide data on the frequency which *Taricha spp.* are ingested, and demonstrate animal interactions affect life history traits.

Thamnophis sirtalis from SLP often used aggressive displays, including directed biting, hissing, and body displays to influence the position of other snakes. Aggression was seen towards con and counter-specific *Thamnophis spp. Thamnophis elegans* from SLP also had several aggressive displays towards *T. sirtalis* but no aggression was directed towards *T. atratus*. *Thamnophis atratus* from SLP did not display aggression during any observation. The data indicate that *T. sirtalis* is the dominant snake at SLP and tend to occupy a preferred habitat according to alone trials. When alone, *T. atratus* occupied the preferred zone, zone 4, for the majority of the observations. However, when *T. sirtalis* was added to the chamber, *T. atratus* occupied the zone 1 more than expected. It was often through direct interaction and aggression that *T. sirtalis* influenced the position of *T. atratus*. *Thamnophis sirtalis* also influenced the position of *T. elegans.* When in the chamber alone, *T. elegans* occupied zones 3 and 4 more than expected. The addition of *T. sirtalis* provoked a change in the space occupation of *T. elegans* to zone 1 more than expected.

Other localities tested for behavioral interactions did not show the same pattern as SLP. Both LC and LM animals showed no spatial occupation changes upon addition of another animal, and no aggression was observed at either LC or LM. This supports the idea that animals at SLP are exhibiting unique behavioral interaction that may affect their life history traits.

The diet of both *T. sirtalis* and *T. atratus* from SLP did not vary significantly. Anurans were the primary food for *T. sirtalis* and *T. atratus*. *Thamnophis elegans*, on the other hand, consumed mammals as their primary food. The majority of *T. atratus* used in the diet study were collected from ponds that do not have a large population of *T. sirtalis.* When not sympatric with *T. sirtalis, T. atratus* were found at the edge of ponds, making the possibility of ingesting anurans easier. Ponds that had both *species, T. atratus* were far removed from the pond edge and had annelids and slugs as the primary food. This may be a direct result of the aggression displayed by *T. sirtalis.*

Thamnophis elegans were also far removed from pond edge when sympatric with *T. sirtalis.* The diet analysis indicates that *T. elegans* is a small mammal specialist. My research shows that *T. elegans* prefers the pond edge and the presence of *T. sirtalis* will directly affect this spatial occupation. Further supporting the affect that the unique interactions at SLP are affecting the snake's ecology.

Historical diet data revealed similar dietary trends among the three species of *Thamnophis*. *Thamnophis sirtalis* and *T. atratus* consumed anurans as their primary food source. The diet of *T. elegans*, however, differed from that found at SLP. Contrary to the diet of *T. elegans* as SLP, the historical data shows that *T. elegans* is the most general predator of the three snakes, having no preference towards any specific category of prey. It was also noted in the historical data set that the majority of locales did not have both *T. sirtalis* and *T. atratus*. This may possibly reflect previous behavioral interactions.

The behavioral interactions that I have seen at SLP may be directly affecting the biology of *T. atratus*. The majority of *T. atratus* at SLP were located primarily around one pond where *T. sirtalis* was not found. The aggressive nature of *T. sirtalis* may have forced *T. atratus* to locate to an area yet to be occupied by *T. sirtalis*. Several ponds throughout SLP had populations of both *T. sirtalis* and *T. atratus*, they were not, however, found occupying the same habitat. *Thamnophis atratus*, at these ponds were located more than 20 meters from the waters edge and *T. sirtalis* were located within 5 meters of the waters edge. Ponds that only had *T. atratus* had all of the snakes within 2 meters of the waters edge. Ponds that had only *T. sirtalis* had snakes located within 20 meters of the waters edge. The habitat segregation that has been seen may be a direct result of the aggressive nature of *T. sirtalis* that had been observed in the behavior experiment.

Throughout California *T. sirtalis* and *T. atratus* have similar diets. However, there are very few localities where these snakes coexist with direct contact. This may be a result of previous territoriality exhibited by one species. Forcing one species to occupy a habitat that it would normally not choose.

Thamnophis elegans has historically been known to have the most general diet of any of the three species observed in these studies. However, I have shown that at SLP, a locality where territoriality is being actively displayed, *T. elegans* diet is very specific towards small mammals. This may be a direct result of *T. sirtalis* actively influencing the habitat occupation of *T. elegans*. This aggression may be forcing *T. elegans* to consume a prey that is costly to handle (Gregory et al. 1980). The historical data set does not indicate that any segregation is occurring between *T. elegans* and any other species. The generalist diet that has historically been noted and is seen in this study may be fostering the coexistence that is seen throughout California.

Interspecific interactions are currently shaping the biology of the snakes at SLP. Historically, interspecific interactions may be responsible for the trends that we currently observe in *Thamnophis spp.* Unfortunately we are unable to witness past events, except through current trends. However, the snakes at SLP may be exhibiting behaviors that have shaped the life histories of garter snakes throughout California and provides us with the opportunity to observe and ask questions that we have only been able to speculate.

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APPENDICES

Appendix A. Tables

Table A1. Chi-square contingency table and P values for comparisons of association between before and after position of garter snakes (Thamnophis spp.) after addition of another snake, and position comparison of two snakes.

Species composition	p-value	Degrees of freedom
TATS SLP 05		
T. atratus before v after	0.06	3
T. atratus v *T. sirtalis*	0.005	3
TSTA SLP 05		
T. sirtalis before v after	0.292	3
T. sirtalis v *T. atratus*	…….	3
TATS SLP 05+06		
T. atratus before v after	0.00012	3
T. atratus v *T. sirtalis*	1.97×10^{-5}	3
TETS SLP wtl 06		
T. elegans before v after	0.0004	3
T. elegans v *T. sirtalis*	…….	3
TATS SLP pd 06		
T. atratus before v after	0.001	3
T. atratus v *T. sirtalis*	0.0007	3
TCTS LC 05		
T.couchii before v after	0.574	3
T.couchii v *T. sirtalis*	0.0019	3
TSTC LC 05		
T. sirtalis before v after	0.037	3
T. sirtalis v *T. couchii*	4.57×10^{-5}	3

Table A2. Diets of *Thamnophis atratus, T. elegans,* and *T. sirtalis* collected from 2004 to 2006 at the Santa Lucia Preserve. N = the total number of snakes captured and examined for stomach contents. Number of stomachs refers to the number of stomachs containing prey of a particular kind.

			Anuran		Fish		Leech		Slug		Salamander		Mammal		Other	
Species	N	# Empty	# stomach	# Items	# stomach	# Items	# stomach	# Items	# stomach	# Items	# stomach	# Items	# stomach	# Items	# stomach	# Items
T. a.	150	75	60	121	0	0	1	1	2	7	14	19	0	0	5	5
T. e.	19	13	0	0	0	0	0	0	0	0	0	0	5	5	1	1
T. s.	44	31	9	18	0	0	0	0	0	0	1	1	0	0	1	1

Table A3. Diets of *Thamnophis atratus, couchii, elegans, ordinoides,* and *sirtalis* collected from 1972 to 2006 by Steve Arnold and others. N = the total number of snakes captured and examined for stomach contents. Number of stomachs refers to the number of stomachs containing prey of a particular kind.

			Anuran		Fish		Leech		Slug		Salamander		Mammal		Other	
Species	N	# Empty	# stomach	# Items	# stomach	# Items	# stomach	# Items	# stomach	# Items	# stomach	# Items	# stomach	# Items	# stomach	# Items
T.a.	93	66	24	122	2	2	0	0	0	0	2	2	0	0	0	0
T.c.	547	423	44	60	36	106	0	0	0	0	1	1	0	0	4	4
T.e.	3003	2159	198	649	323	561	82	266	203	759	11	11	19	26	19	65
T.o.	21	15	0	0	0	0	0	0	4	4	3	3	0	0	0	0
T.s.	290	200	63	260	5	10	6	11	0	0	21	26	0	0	0	0

Appendix B. Figures

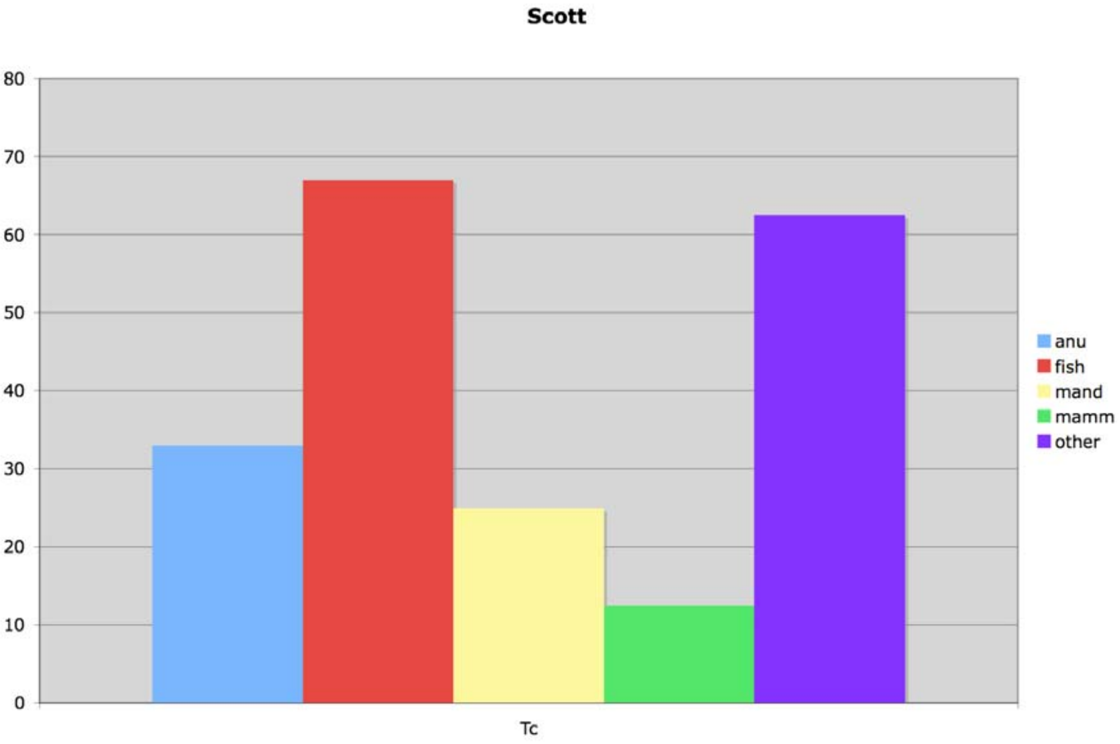

Fig. B1. Percentage of prey in the stomachs of *T. couchii* at Scott locale.

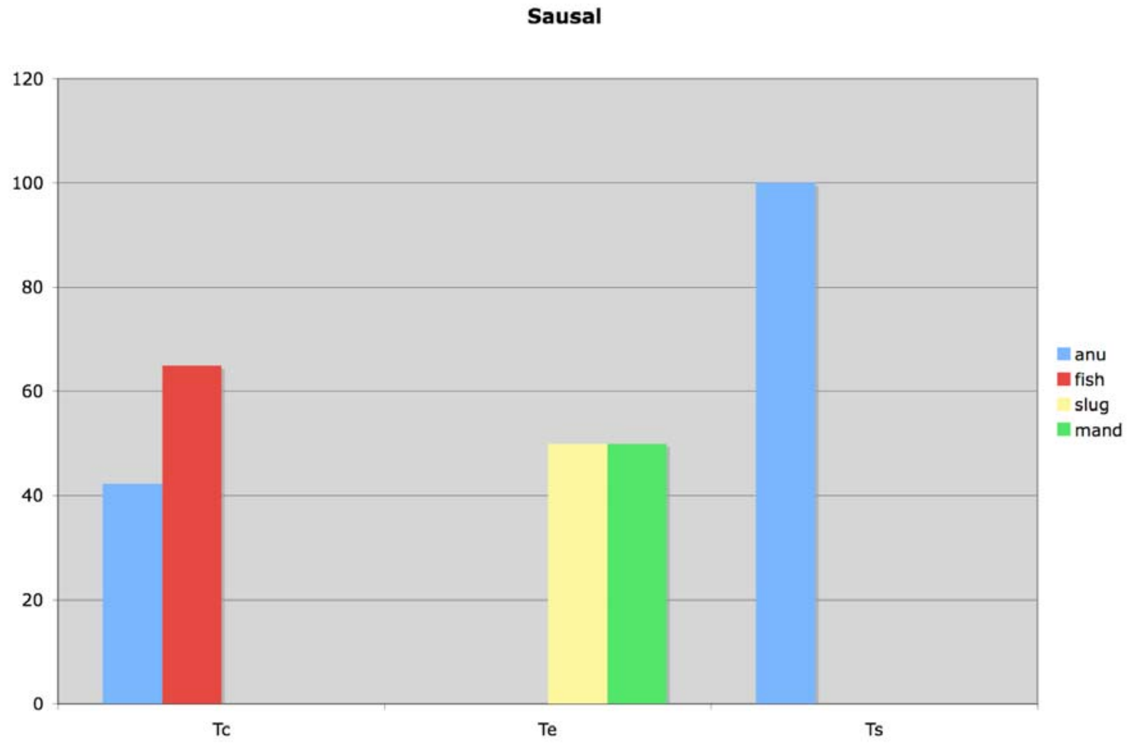

Fig. B2. Percentage of prey in the stomachs of *T. elegans, T. sirtalis,* and *T. couchii* at Sausal locale. The diets of the snakes varied significantly based on the number of stomachs ($p=1.6 \times 10^{-6}$).

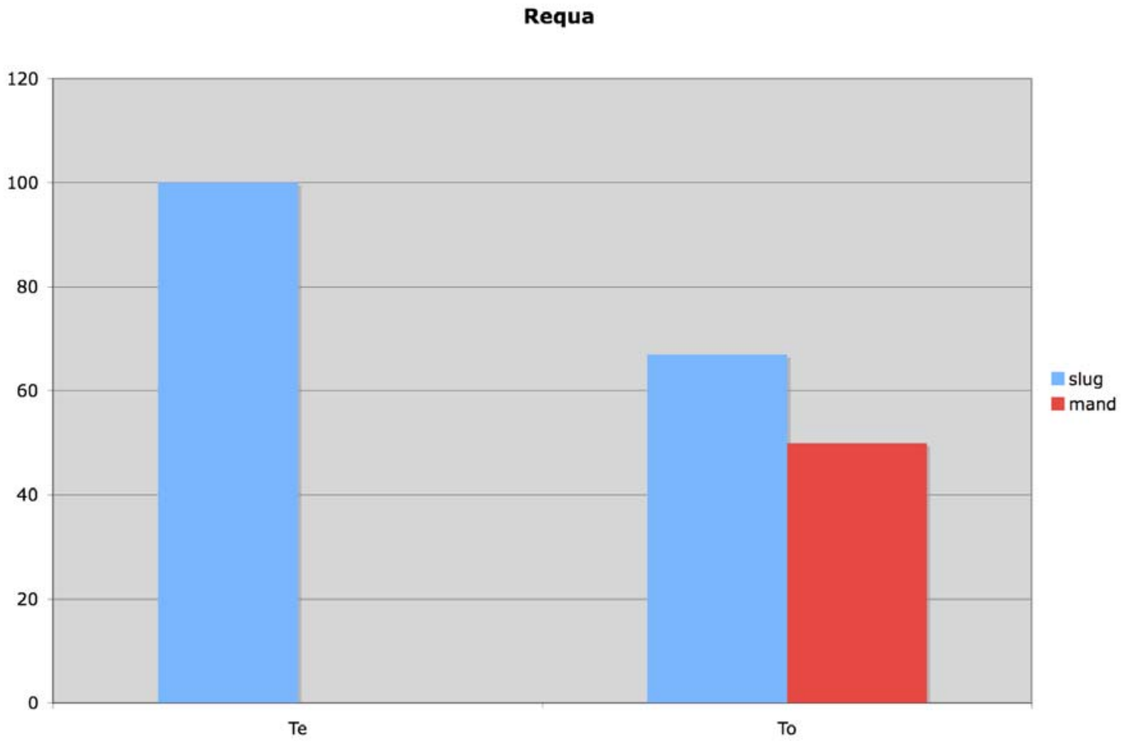

Fig. B3. Percentage of prey in the stomachs of *T. elegans* and *T. ordinoides* at Requa locale. The diets of the snakes did not vary significantly based on the number of stomachs (p=0.125).

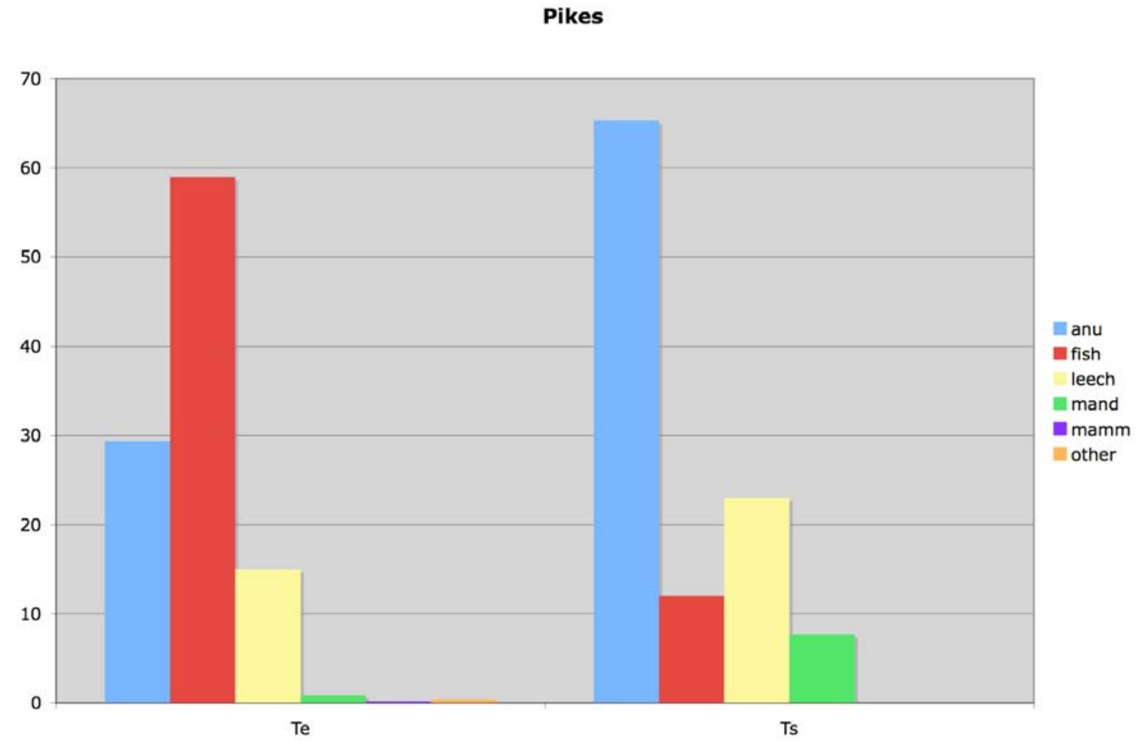

Fig. B4. Percentage of prey in the stomachs of *T. elegans*, and *T. sirtalis*, at Pikes locale. The diets of the snakes varied significantly based on the number of stomachs ($p=1.4x10^{-5}$).

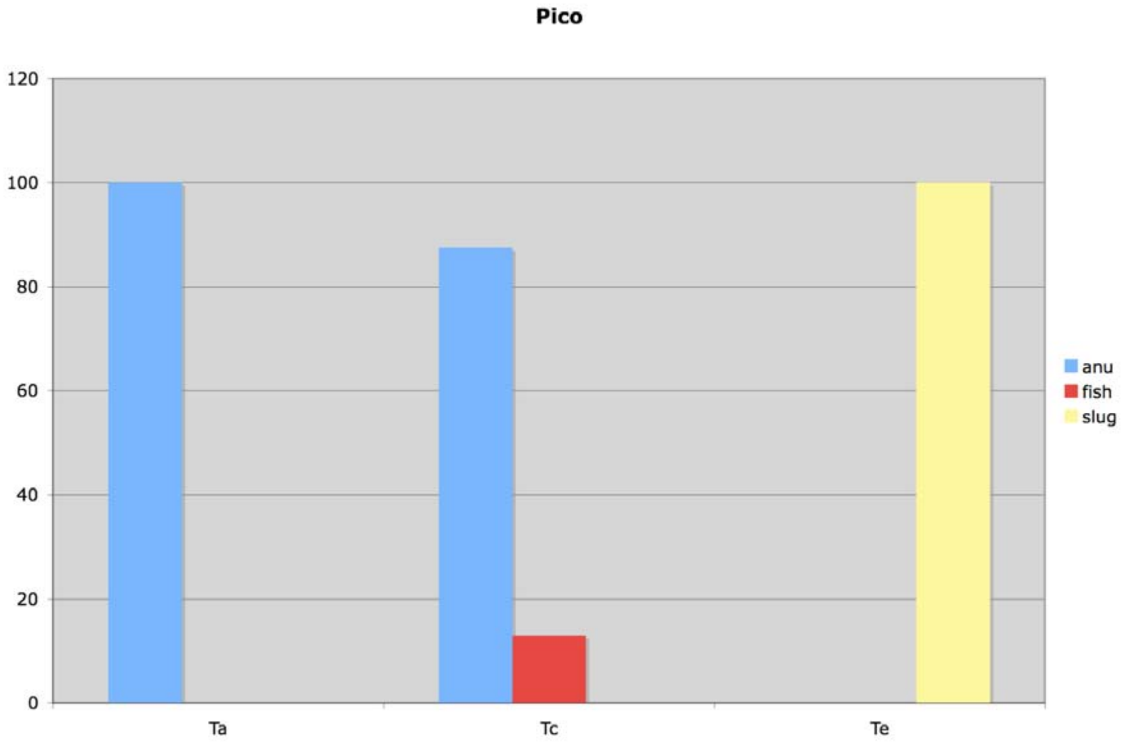

Fig. B5. Percentage of prey in the stomachs of *T. elegans, T. atratus,* and *T. couchii* at Pico locale. The diets of the snakes did not vary significantly based on the number of stomachs (p=0.023).

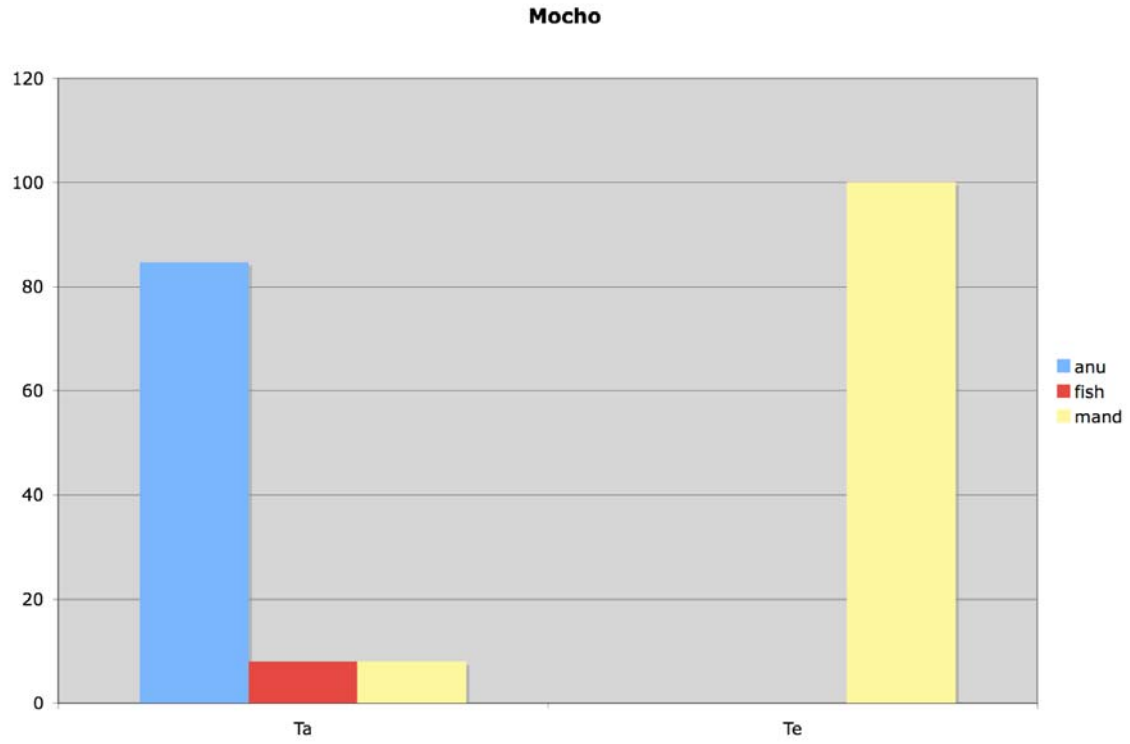

Fig. B6. Percentage of prey in the stomachs of *T. elegans*, *T. sirtalis,* and *T. atratus* at Mocho locale. The diets of the snakes varied significantly based on the number of stomachs (p=0.016).

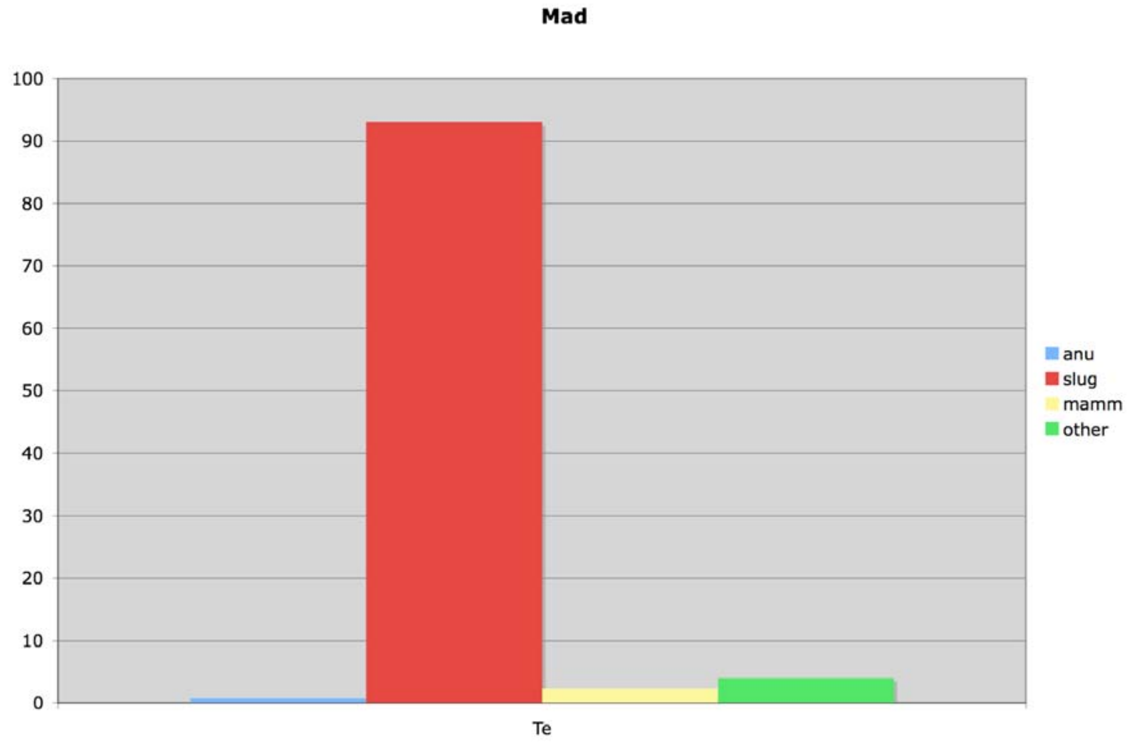

Fig. B7. Percentage of prey in the stomachs of *T. elegans* at Mad locale.

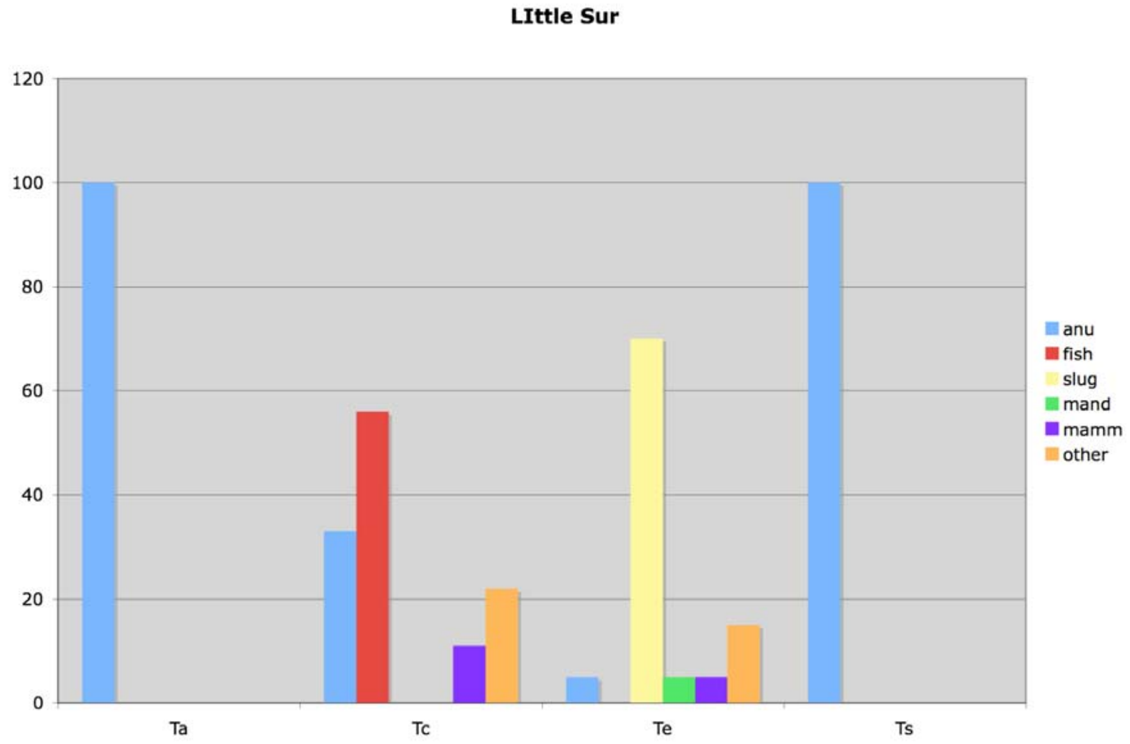

Fig. B8. Percentage of prey in the stomachs of *T. elegans, T. sirtalis, T. atratus* and *T. couchii* at Little Sur locale. The diets of the snakes varied significantly based on the number of stomachs (p=0.00352).

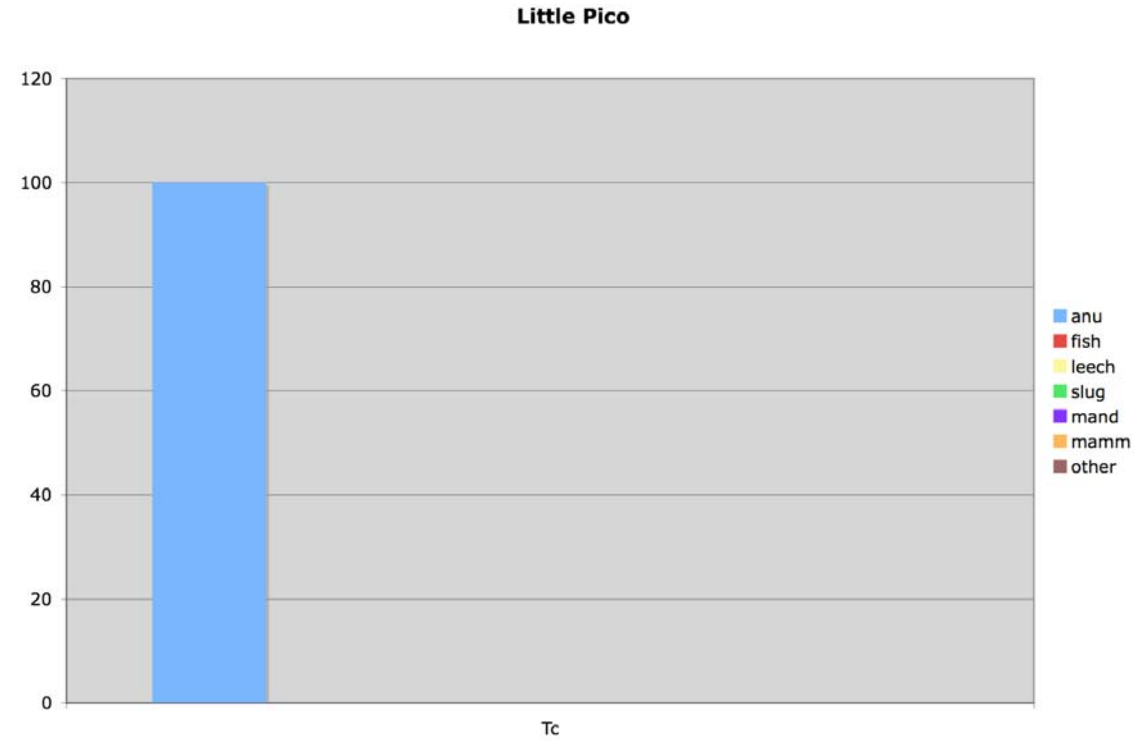

Fig. B9. Percentage of prey in the stomach of *T. couchii* at Little Pico locale.

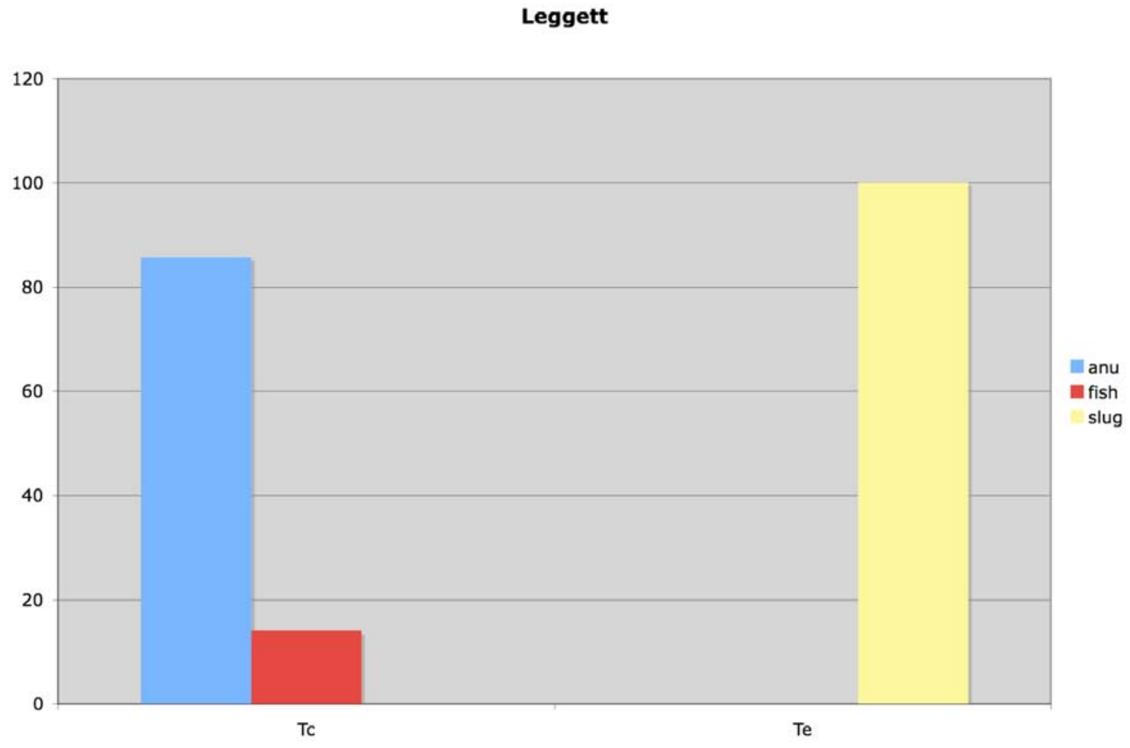

Fig. B10. Percentage of prey in the stomachs of *T. elegans, T. sirtalis,* and *T. couchii* at Leggett locale. The diets of the snakes varied significantly based on the number of stomachs (p=0.0003).

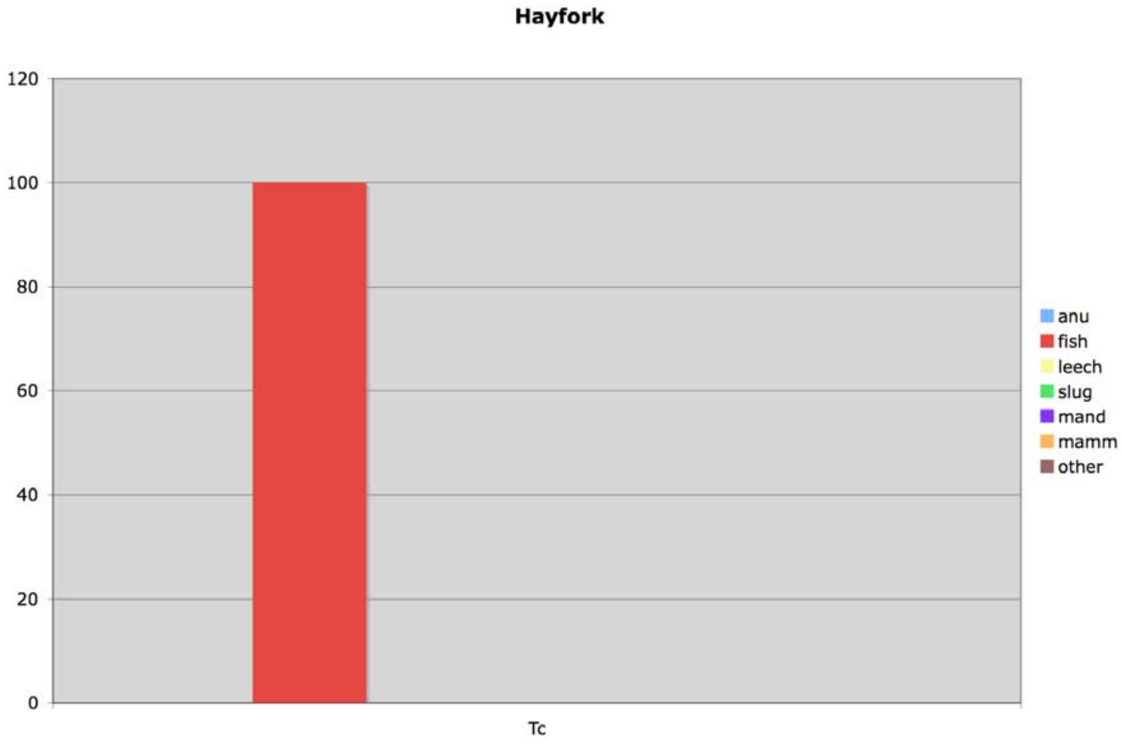

Fig. B11. Percentage of prey in the stomach of *T. couchii* at Hayfork locale.

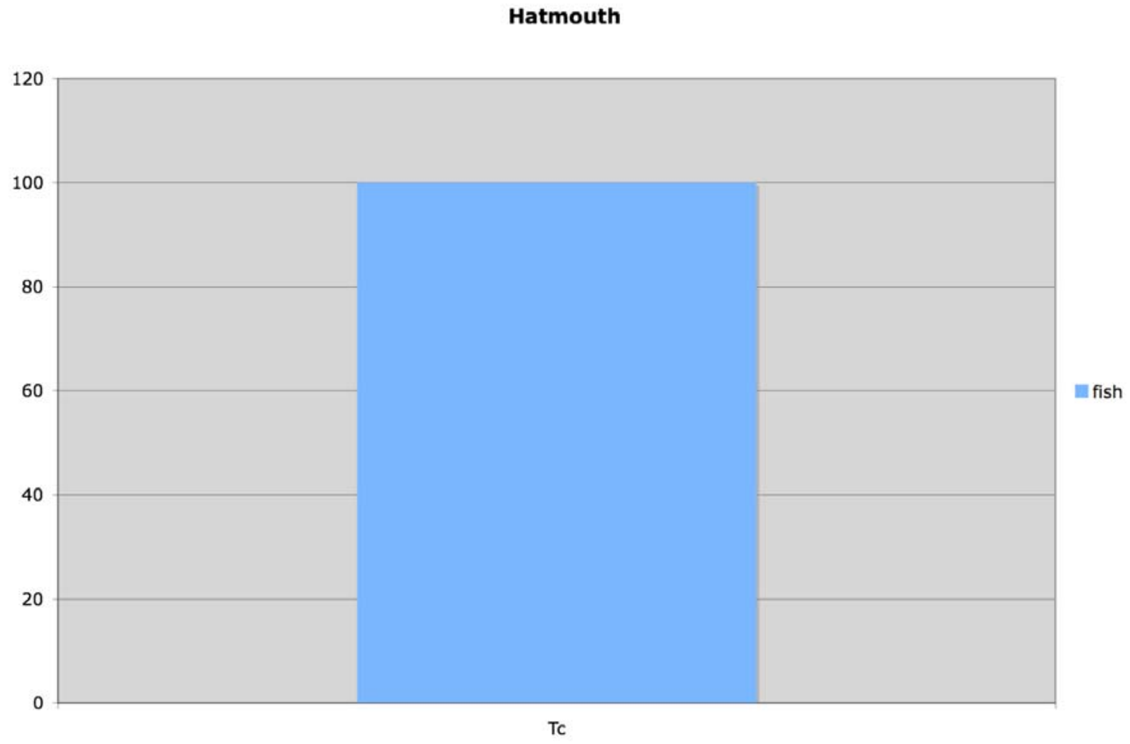

Fig. B12. Percentage of prey in the stomachs of *T. couchii* at Hatmouth locale.

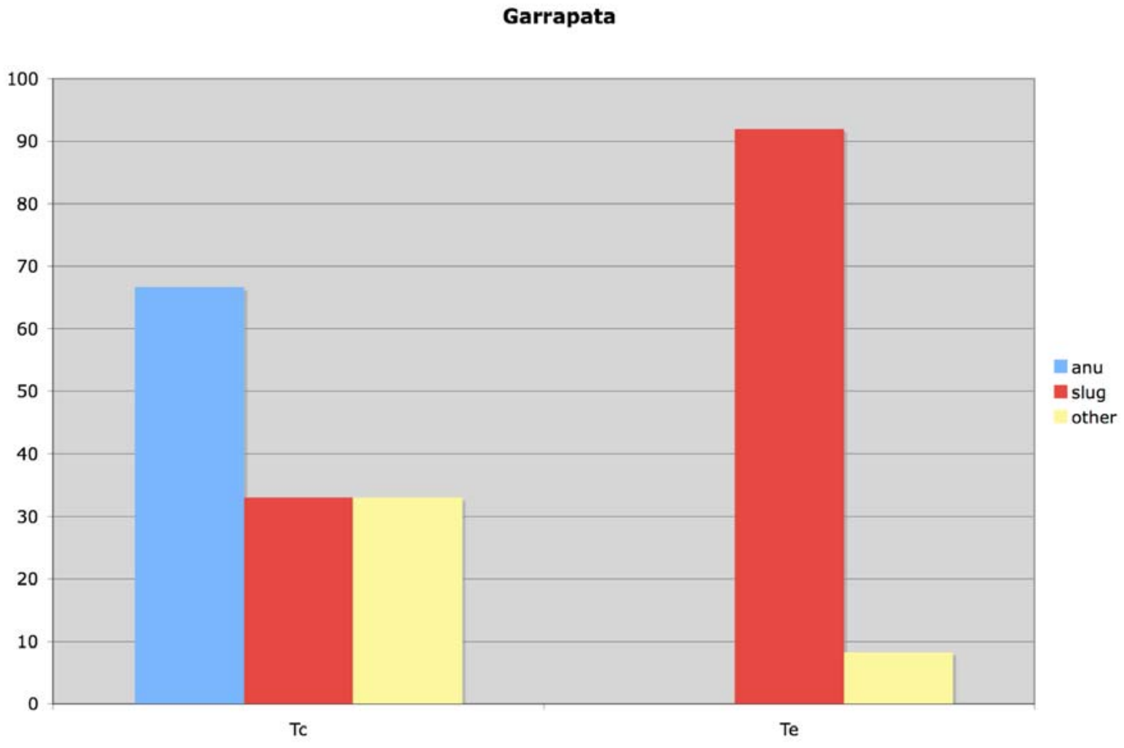

Fig. B13. Percentage of prey in the stomachs of *T. elegans* and *T. couchii* at Garrapata locale. The diets of the snakes did not vary significantly based on the number of stomachs (p=0.015).

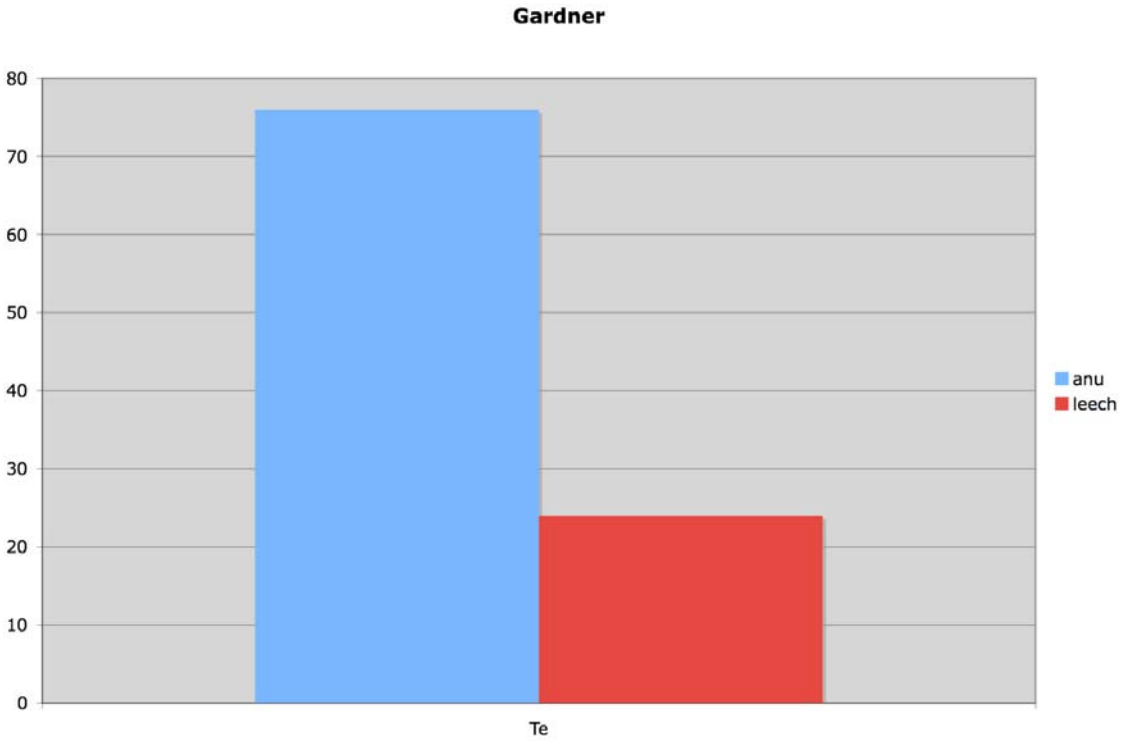

Fig. B14. Percentage of prey in the stomachs of *T. elegans* at Gardner locale.

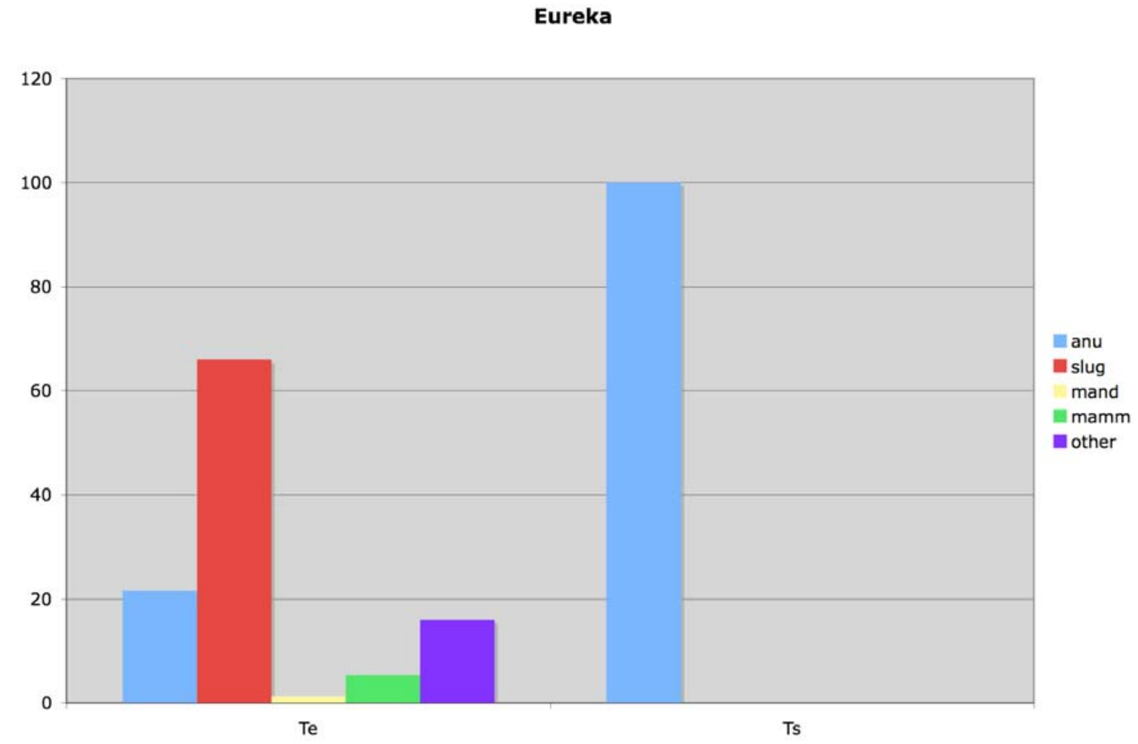

Fig. B15. Percentage of prey in the stomachs of *T. elegans* and *T. sirtalis* at Eureka locale. The diets of the snakes did not vary significantly based on the number of stomachs (p=0.029).

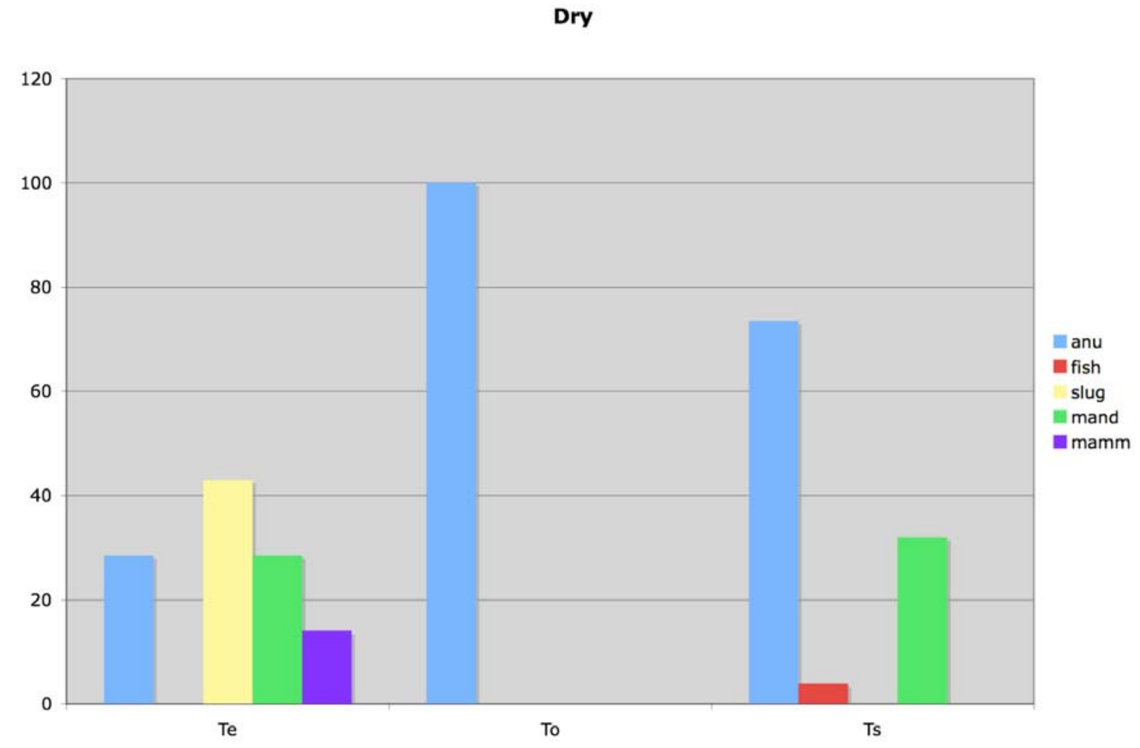

Fig. B16. Percentage of prey in the stomachs of *T. elegans, T. sirtalis,* and *T. ordinoides* at Dry locale. The diets of the snakes varied significantly based on the number of stomachs ($p=8x10^{-5}$).

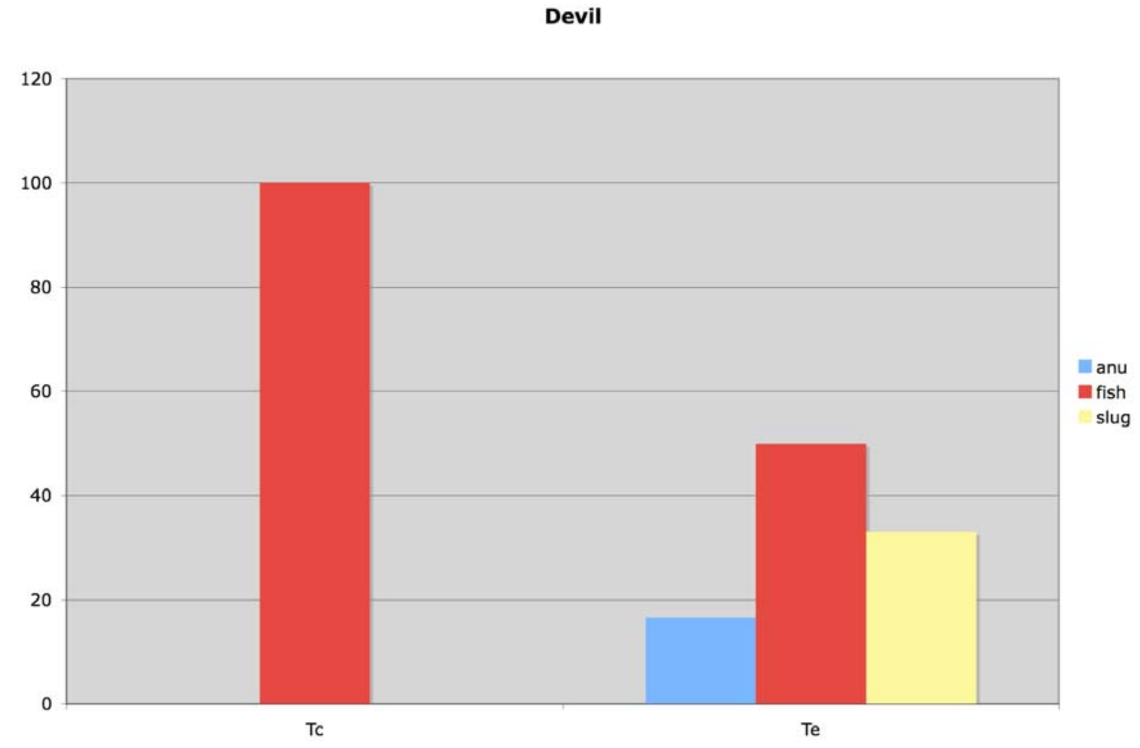

Fig. B17. Percentage of prey in the stomachs of *T. elegans* and *T. couchii* at Devil locale. The diets of the snakes varied significantly based on the number of stomachs (p=0.0355).

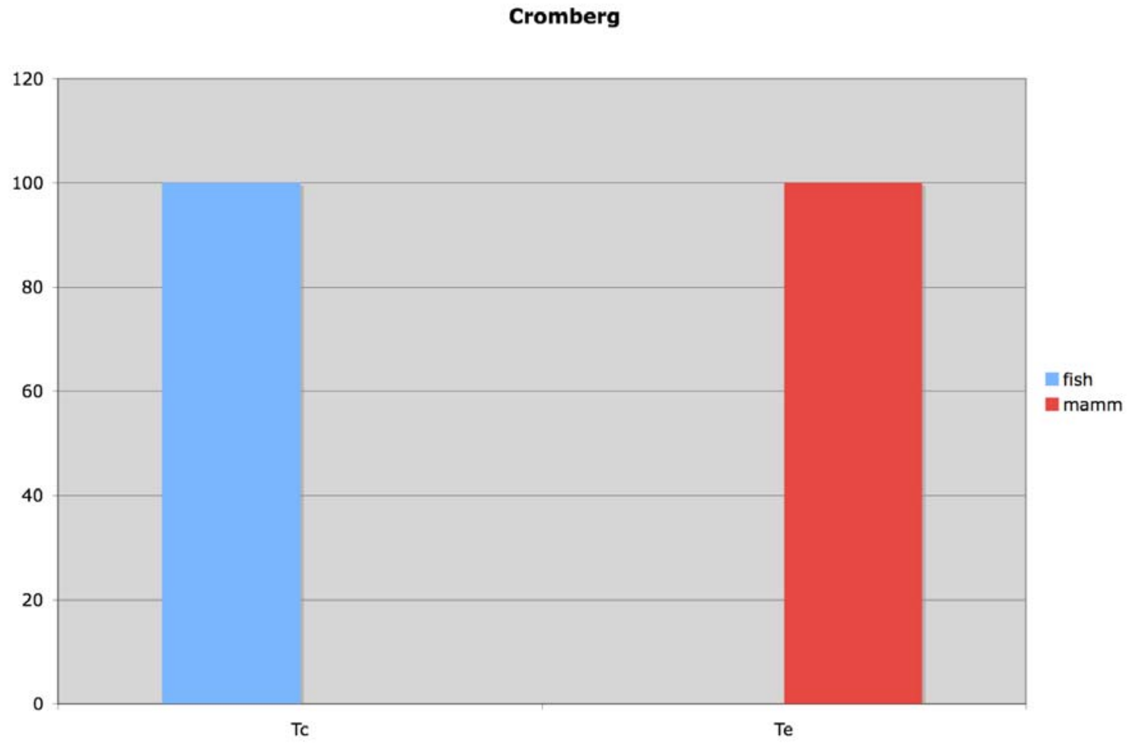

Fig. B18. Percentage of prey in the stomachs of *T. elegans* and *T. couchii* at Cromberg locale. The diets of the snakes varied significantly based on the number of stomachs ($p=5.7x10^{-7}$).

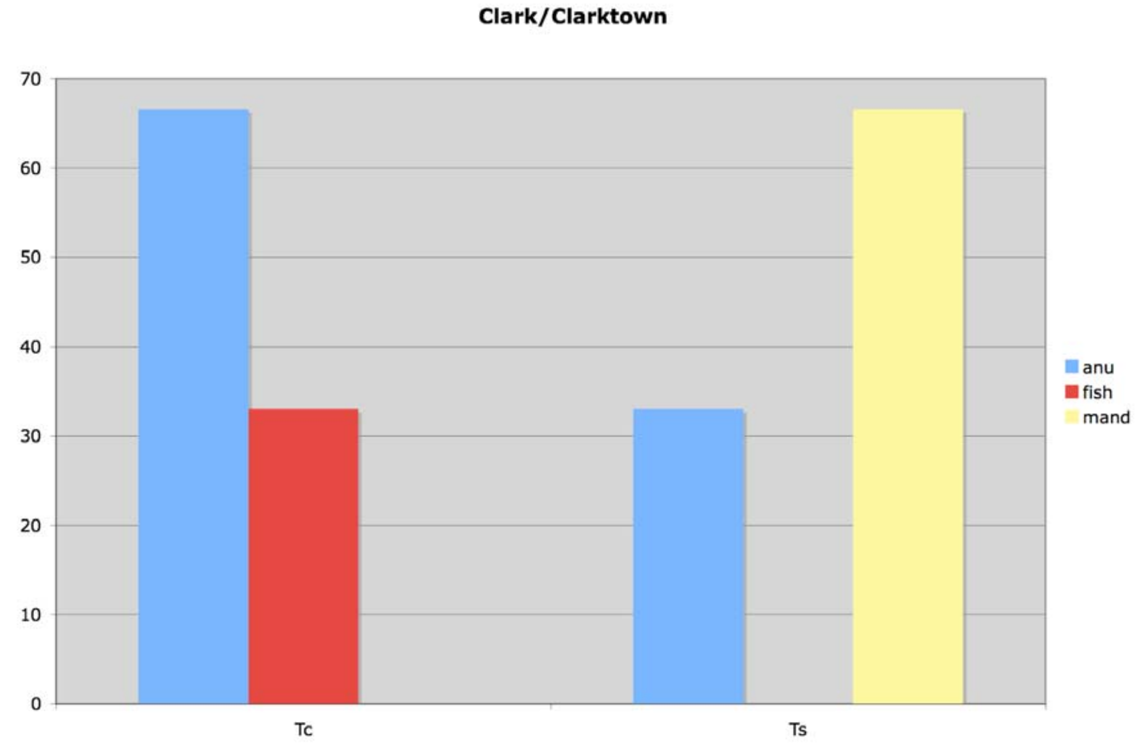

Fig. B19. Percentage of prey in the stomachs of *T. sirtalis* and *T. couchii* at Clark/Clarktown locale. The diets of the snakes did not vary significantly based on the number of stomachs (p=0.155).