

3-2011

Comparative Biology of Sympatric Red Diamond and Southern Pacific Rattlesnakes in Southern California

Eric Allen Dugan

Follow this and additional works at: <http://scholarsrepository.llu.edu/etd>



Part of the [Biology Commons](#)

Recommended Citation

Dugan, Eric Allen, "Comparative Biology of Sympatric Red Diamond and Southern Pacific Rattlesnakes in Southern California" (2011). *Loma Linda University Electronic Theses, Dissertations & Projects*. 234.
<http://scholarsrepository.llu.edu/etd/234>

This Dissertation is brought to you for free and open access by TheScholarsRepository@LLU: Digital Archive of Research, Scholarship & Creative Works. It has been accepted for inclusion in Loma Linda University Electronic Theses, Dissertations & Projects by an authorized administrator of TheScholarsRepository@LLU: Digital Archive of Research, Scholarship & Creative Works. For more information, please contact scholarsrepository@llu.edu.

LOMA LINDA UNIVERSITY
School of Science and Technology
in conjunction with the
Faculty of Graduate Studies

Comparative Biology of Sympatric Red Diamond and
Southern Pacific Rattlesnakes in Southern California

by

Eric Allen Dugan

A Dissertation submitted in partial satisfaction of
the requirements for the degree of
Doctor of Philosophy in Biology

March 2011

© 2011

Eric Allen Dugan
All Rights Reserved

Each person whose signature appears below certifies that this dissertation in his/her opinion is adequate, in scope and quality, as a dissertation for the degree Doctor of Philosophy.

_____, Chairperson
William K. Hayes, Professor of Biology

Leonard R. Brand, Professor of Biology and Paleontology

Sean P. Bush, Professor of Emergency Medicine, School of Medicine

L. Lee Grismer, Professor of Biology, La Sierra University

Bradford D. Martin, Professor of Physical Therapy, School of Allied Health Professions

ACKNOWLEDGEMENTS

There are so many that I owe much to. I am forever indebted to this group of people, without whom I would certainly have never completed this venture. First and foremost is my wife, Sandie. She has sacrificed in many ways that I could not do justice in summarizing. She has been an incredible inspiration to me, showing me time and time again what hard work and dedication can achieve in life. You are an amazing mother to Delaney and Caleb, more so that I could have guessed. This accomplishment is just as much yours as it is mine. I love you, Sandie!

My parents, Ron and Teri, facilitated and supported my passion and unending love for field work and for snakes. They allowed me to keep snakes as a kid and drove me long distances into remote corners of southern California to search for them. Thank you mom and dad, your love has always been felt. I cannot thank you enough for that. I love you guys more than I have ever said.

Dave Lohr, Gary Keasler, and Barney Tomberlin endured endless questions from a teenage kid trying to learn more about the subjects that have always captivated him. Whether it was driving remote sections of San Diego County looking for snakes with Dave, being told where and when to go in Baja by Gary, or being given the opportunity to live with Barney in Portal, Arizona, for two summers, all of these experiences have helped shaped me and my interests. Rob Lovich was instrumental in my early years at Loma Linda and has provided support and encouragement throughout my time here. He was also invaluable in my consulting work on Marine Corps Base Camp Pendleton, I thank you for that! No list of important people in my life would be complete without mention of Chris Rodriguez. Together, we spent years exploring the southwestern United

States, and Sonora and Baja, Mexico. I have yet to meet a person with the same tenacity that Chris has in the field. He was also there to laugh at my tumbling down a hillside and landing in cactus while radio-tracking rattlesnakes. Thank you my brother, I look forward to many more years of the same.

Dr. Bill Hayes has been a gift from above: from accepting a young graduate student into his lab that he knew little about, to mentoring and providing me an opportunity to study rattlesnakes in a field setting. I have yet to come across a person with his mastery of biological statistics and ability to turn my average manuscripts into documents worthy of publication. You have certainly managed me well as both a student and a person. You are single-handedly responsible for getting me to the finish line.

I would also like to thank my committee members for their advice and direction. Dr. Lee Grismer, you have been a tremendous inspiration during our time spent together. There is no doubt in my mind that you are one of the world's present-day pioneers of herpetology. Your herpetology class taught me how much I didn't know; your production of papers and discovery of new species is hard to comprehend in the modern era. Dr. Leonard Brand was a calming and supportive figure throughout. I will never forget your mammalogy course, as it will go down as one the best courses I have taken at any level of my course work. Dr. Sean Bush was critical in the early stages of my field work. You provided me with equipment and surgical techniques I relied on throughout my field work. It was also reassuring to know you were always available in case of snake bite. Dr. Brad Martin was gracious enough to join my committee and provide his expertise of biological competition and symbiosis. I thank you for that.

To those in the Hayes lab whom I have collaborated with, I thank you, too. Alex Figueroa was especially supportive in my field work and writing efforts. He has since remained a good friend, one that I will certainly be collaborating with on future projects. Dr. Zia Nisani has been a fantastic model student and an exceptional and caring friend. He also was instrumental in my teaching experience at Antelope Valley College. Aaron Corbit generously assisted with various statistical analyses.

CONTENTS

Approval Page.....	iii
Acknowledgements.....	iv
Table of Contents.....	vii
List of Figures.....	x
List of Tables.....	xii
Abstract.....	xiii
Chapter	
1. Introduction to Snake Resource Use and Niche Partitioning.....	1
Niche Theory.....	1
Niche Partitioning by Vipers.....	4
Space Use.....	5
Temporal Resources.....	6
Thermal Resources.....	7
Diet.....	8
Niche Partitioning by <i>Crotalus ruber</i> and <i>C. oreganus helleri</i>	10
References.....	14
2. Home Range Size, Movements, and Mating Phenology of Sympatric Red Diamond (<i>Crotalus ruber</i>) and Southern Pacific (<i>C. oreganus helleri</i>) Rattlesnakes in Southern California.....	20
Abstract.....	21
Introduction.....	22
Materials and Methods.....	25
Study Site.....	25
Radio-telemetry.....	26
Home Range Size and Movements.....	27
Mating Phenology.....	29
Statistical Analyses.....	29
Results.....	31

Home Range Size.....	31
Autocorrelation	34
Movements.....	34
Mating Phenology.....	38
Discussion.....	39
Home Range Size.....	39
Movements and Mating Phenology	41
Niche Partitioning.....	44
Acknowledgments.....	45
References.....	46
3. Niche Separation and Resource Partitioning in the Sympatric Rattlesnakes <i>Crotalus ruber</i> and <i>C. oreganus helleri</i> in Southern California	52
Abstract.....	53
Introduction.....	54
Material and Methods	57
Study Species.....	57
Study Site.....	58
Radio-telemetry.....	59
Macrohabitat Use.....	60
Microhabitat Use.....	62
Thermal Resources.....	62
Activity and Temporal Resource Use.....	64
Diet.....	65
Niche Overlap.....	66
Results.....	67
Macrohabitat Use.....	67
Microhabitat Use.....	71
Thermal Resources.....	71
Activity and Temporal Resource Use.....	73
Diet.....	77
Niche Overlap.....	80
Discussion.....	83
Macrohabitat Use.....	84
Microhabitat Use.....	87
Thermal Resources.....	88

Temporal Resources.....	89
Dietary Resources.....	89
Niche Overlap.....	91
Acknowledgements.....	92
References.....	93
4. Diet and Feeding Ecology of the Red Diamond Rattlesnake, <i>Crotalus</i> <i>ruber</i> (Serpentes: Viperidae).....	103
Abstract.....	104
Introduction.....	105
Materials and Methods.....	107
Sources of Prey Items.....	107
Identification of Prey Items.....	109
Sources of Dietary Variation.....	111
Analyses.....	111
Results.....	112
Prey Items.....	112
Predator Size Distribution.....	115
Ontogenetic Variation.....	115
Sexual Variation.....	117
Geographic Variation.....	119
Seasonal Variation.....	120
Discussion.....	120
Acknowledgements.....	126
References.....	128
Appendix.....	137
5. Conclusions and Discussion.....	138
References.....	143

FIGURES

Figure	Page
2.1 Mean fixed kernel estimates of home range size for <i>Crotalus ruber</i> and <i>C. oreganus helleri</i> at Chino Hills State Park, California.....	33
2.2 Mean daily movements per month of <i>Crotalus ruber</i> (dashed lines) and <i>C. oreganus helleri</i> (solid lines).	35
3.1 Satellite image of study area in Chino Hills State Park, southern California, illustrating the heterogeneous distribution of the five macrohabitats. Inset: study site in relation to southern California counties.	59
3.2 Spatial axis: Macrohabitat availability versus macrohabitat use by radio-telemetered <i>Crotalus ruber</i> ($n = 9$) and <i>C. o. helleri</i> ($n = 9$) during the active season (March–November)	68
3.3 Spatial axis: Macrohabitat characteristics (distances to nearest macrohabitat type, mean ± 1 SE) of individual locations used by <i>Crotalus ruber</i> ($n = 57$) and <i>C. o. helleri</i> ($n = 70$) during the (A) active and (B) winter seasons	70
3.4 Thermal axis: thermal attributes (mean ± 1 SE) of locations occupied by <i>Crotalus ruber</i> ($n = 49$) and <i>C. o. helleri</i> ($n = 78$).....	72
3.5 Temporal axis: Comparison of activities exhibited (percentage of observations, mean ± 1 SE) by radio-telemetered <i>Crotalus ruber</i> ($n = 8$) and <i>C. o. helleri</i> ($n = 9$).	74
3.6 Temporal axis: Seasonal variation of movements (mean ± 1 SE) by radio-telemetered adult male <i>Crotalus ruber</i> ($n = 6$) and <i>C. o. helleri</i> ($n = 6$)	75
3.7 Temporal axis: Circadian activity (percent of observations, mean ± 1 SE) of <i>C. ruber</i> ($n = 8$) and <i>C. o. helleri</i> ($n = 9$) in Chino Hills State Park.	76
3.8 Dietary axis: Prey size class utilization by radio-telemetered, opportunistically encountered, and road-killed <i>Crotalus ruber</i> and <i>C. o. helleri</i> . Prey size classes are based on the adult size of prey species.	81

4.1	Locations of red diamond rattlesnake (<i>Crotalus ruber</i>) specimens yielding prey items from coastal (unfilled circles) and desert (filled circles) populations in California (USA) and the two states of Baja California (Mexico). Numbers of specimens having only regional locality data are indicated within parentheses; habitat types were not assigned to these	110
4.2	Predator-prey size relationships for three major food types of the red diamond rattlesnake (<i>Crotalus ruber</i>).....	117
4.3	Comparison of predator-prey size relationships between male and female red diamond rattlesnakes (<i>Crotalus ruber</i>).	118
4.4	Percentage of red diamond rattlesnakes (<i>Crotalus ruber</i>) containing food items during each month (no data were available for January). Note the consumption of food items year-round.....	121

TABLES

Table		Page
2.1	Summary number of locations, home range estimates, mean daily movements, and Schoener’s autocorrelation for red diamond (<i>Crotalus ruber</i>) and southern Pacific (<i>C. oreganus helleri</i>) rattlesnakes.	32
2.2	Summary of analysis of variance results for home range estimates, mean daily movements, and autocorrelation for two species of rattlesnake over three seasons... ..	37
2.3	Number of sexual interactions observed in red diamond (<i>Crotalus ruber</i>) and southern Pacific (<i>C. oreganus helleri</i>) rattlesnakes during spring and late Summer/Fall.....	38
3.1	Number of prey items per taxon consumed by sympatric <i>Crotalus ruber</i> and <i>C. oreganus helleri</i> in Chino Hills State Park, California.....	78
3.2	Pianka’s and Czekanowski’s niche overlap values for major niche axes resulting from pairwise comparisons between sympatric <i>Crotalus ruber</i> and <i>C. oreganus helleri</i>	83
4.1	Prey consumed by <i>Crotalus ruber</i> , including frequency (<i>n</i>), proportion of total items, and proportion of identifiable items within classes Aves, Mammalia, and Reptilia.	114

ABSTRACT OF THE DISSERTATION

Comparative Biology of Sympatric Red Diamond and Southern Pacific Rattlesnakes in Southern California

by

ERIC ALLEN DUGAN

Doctor of Philosophy, Graduate Program in Biology
Loma Linda University, March 2011
Dr. William K. Hayes, Chairperson

I compared the biology of two sympatric rattlesnakes within the context of resource use and niche partitioning. Using radio-telemetry and mark-recapture involving passive integrated transponders (PIT) tags, I studied Red Diamond (*Crotalus ruber*) and Southern Pacific (*C. oreganus helleri*) Rattlesnakes in Chino Hills State Park, California, from March 2003 through March 2010.

The first of three studies compared the two species in terms of home range size, movements, and mating phenology. *Crotalus o. helleri* occupied larger home ranges than *C. ruber*, and exhibited 1.9–2.8-fold greater movement distances (depending on year) than *C. ruber*. Mating phenology also varied, with *C. ruber* mating only in spring, and *C. o. helleri* exhibiting a spring and fall bi-modal mating system.

The second study examined interspecific differential resource use. I compared both species along all four major niche axes (spatial, temporal, thermal, and diet) to test the general notion that sympatric vipers partition primarily macrohabitat, which contrasts with the general pattern in snakes of partitioning diet. Pianka's and Czekanowski's indices of niche overlap revealed modest overlap in macrohabitat and low overlap in diet;

however, diet may be influenced by macrohabitat and body size differences. The two species exhibited broad overlap of microhabitat, thermal, and temporal (seasonal and circadian) resources. Null model tests using Monte Carlo simulations indicated that only diet (prey size) overlap was significantly less than expected.

My third study examined and described the diet of *C. ruber* throughout the species' range (*C. o. helleri*'s diet had been examined previously) based on trophic data collected from museum specimens, live animals from my Chino Hills study site, road-killed snakes, opportunistic field observations, and existing literature. The diet of *C. ruber* consisted primarily of mammals (91.6%), but also included occasional lizards (7.5%) and birds, with no ontogenetic shift in prey type. Males averaged larger than females. Coastal snakes averaged larger and consumed a higher proportion of rodents and prey of larger body size than snakes from desert populations. Feeding occurred occasionally during winter, even at the northern extreme of its range.

This dissertation provides the most detailed and complete analysis of resource use and niche separation by sympatric North American viper species. If niche partitioning exists among the rattlesnakes studied, I suggest it occurs subtly along more than one axis and has resulted largely from non-competitive interactions. I was unable to detect significant habitat partitioning using contemporary methodologies. These findings call into question the generality of habitat partitioning by vipers (Luiselli, 2006a, 2006b; Luiselli et al., 2007), and suggest the need for further study.

CHAPTER ONE
INTRODUCTION TO SNAKE RESOURCE USE AND NICHE
PARTITIONING

In this dissertation, I use a comparative approach to examine resource use and niche partitioning among two sympatric rattlesnake species in southern California. This chapter introduces and reviews the concepts of niche, niche theory, and niche partitioning by vipers. I then discuss the primary niche axes (spatial, temporal, thermal, and diet) specific to snake communities, and place them within the context of general snake biology. I then provide an overview of my studies of the movements, home range size, mating phenology, resource use, and niche separation of red diamond (*Crotalus ruber*) and southern Pacific (*C. oreganus helleri*) rattlesnakes in Chino Hills State Park, California.

Niche Theory

Developed in the early 1900's, the concepts of "niche" and "niche theory" were introduced to help explain interspecific patterns and relationships in nature. Interpreted today, niche refers to both a species' unique set of characteristics related to its biological functions within a community, as well as to the physical area it occupies. Development of mathematical indices (e.g., Pianka's and Czekanowski's) to measure niche overlap (Feinsinger et al., 1981; Pianka, 1981) has provided a framework for ecologists to examine niche theory within the context of the structure of biological communities.

Competition for resources is a fundamental structuring agent of most natural communities. Traditionally, biologists have suggested differential resource use (niche partitioning) as the mechanism allowing for ecologically similar species to co-exist under conditions of limited resources (Schoener, 1974). Niche shifts often occur where competitors coexist, whereas in the absence of competitors a species may occupy a broader niche (Pianka, 1981). Without such mechanisms in play, the results of competition can be intense, with extreme cases resulting in character displacement (e.g., Darwin's finches; Grant and Grant, 2006) or local extirpation of the less-fit species (e.g., freshwater mussels: Ricciardi et al., 1998; sympatric snakes: Metzger et al., 2009). In his landmark publication, Gause (1934) combined the ideas of natural selection, competition, and niche in his development of the competitive exclusion principle (Gause's Law). Gause's Law contends that two species competing for the same resources cannot stably coexist. Although developed more than six decades ago, his principle remains widely accepted in modern biological theory and pertinent to current research (e.g., Pfennig et al., 2006; Pearman et al., 2007; Metzger et al., 2009).

Ecologists now recognize that mechanisms other than niche partitioning and character displacement can promote coexistence of similar species. Chesson (2000) viewed coexistence mechanisms as either stabilizing or equalizing. *Stabilizing mechanisms* involve species differences that reduce niche overlap to minimize fitness inequalities in competitive interactions (i.e., niche partitioning and character displacement). *Equalizing mechanisms* invoke similar responses of species to environmental conditions (i.e., fitness equivalency, or neutrality), such as dispersal and recruitment limitation (Hurtt and Pacala, 1995; Hubbell, 2005), that reduce competitive

exclusion and allow coexistence from weak stabilizing mechanisms. Following publication of Hubbell's (2001) monograph on neutrality, controversy erupted over the importance of niche and neutral processes to coexistence, though evidence supporting neutral processes has been elusive (e.g., Adler et al., 2007; Cadotte, 2007). More recently, these differences have been treated as a neutrality-niche continuum (Vergnon et al., 2009).

Taking the concept of niche further, one must consider the difference between the "potential" or "fundamental niche" and the "realized niche" (Vandermeer, 1972; Pearman et al., 2007). The realized niche is typically a subset of the fundamental niche. Competition and contact with interspecifics often result in some degree of specialization (e.g., habitat selection or food preference). Ultimately, it is this specialization or niche shift that narrows the fundamental niche into the realized niche. As complete interspecific niche overlap is uncommon and the number of niche dimensions can be substantial, ecosystems can support great diversity even among ecologically similar species (Pianka, 1974; M'Closkey, 1978).

The four primary niche axes are considered to be spatial (micro- and macrohabitat), temporal (diel or seasonal activity patterns), thermal, and dietary resources (Schoener, 1974; Saint-Girons, 1975; Goodyear and Pianka, 2008). Modest niche partitioning along one or two axes appears to provide sufficient separation to allow the sympatric coexistence of competitors. Unfortunately, the majority of efforts to characterize niche use among sympatric species have only focused on one or two of the major axes. The ectothermic and generally sedentary nature of vipers offers great potential to examine all four axes.

Niche Partitioning by Vipers

As increasingly popular models for studies of ecology (Shine and Bonnet, 2000), vipers have been the subjects of many classical studies. However, efforts to examine and detail interspecific resources are surprisingly few. Members of the European genus *Vipera* have yielded the most significant insights into how vipers use environments in the presence of a closely-related interspecific competitor (Saint-Girons, 1975; Monney, 1996; Brito and Crespo, 2002; De Lina, 2006; Martinez et al., 2006; Luiselli et al., 2007).

Two robust reviews of resource partitioning among snakes (Toft, 1985; Luiselli, 2006) have deduced several general patterns and provided a framework for interpretation of observations within the group. Toft (1985) established that sympatric snakes were atypical among vertebrates in that they partition food resources, rather than habitat, a trend supported by recent research (e.g., Goodyear and Pianka, 2008). More recently, Luiselli's review (2006) summarized general trends of interspecific competition and resource partitioning in snake communities on a global scale. Summarizing Luiselli (2006), aquatic snakes from temperate regions primarily partition food types and exhibit broad overlap in habitat use, terrestrial snakes in temperate regions show no generalized pattern, and tropical snakes which face strong interspecific competition partition food resources. Most importantly for my studies, he noted that sympatric vipers are atypical among snakes in that they most often partition habitats, rather than food resources.

North American rattlesnakes (genus *Crotalus*) are amongst the most extensively studied snakes (Beaman and Hayes, 2008); however, very little is known about the comparative biology of sympatric species. The ranges of many species overlap broadly, particularly in the arid and semi-arid regions of southwest North America, where species richness is highest (Klauber, 1972). In his study of sympatric *Crotalus atrox*, C.

molossus, and *C. tigris* in southern Arizona, Beck (1995) described significant differences along the spatial axis, but all three species broadly overlapped along the thermal and temporal axes. Other studies of sympatric rattlesnakes described differences in habitat associations (Pough, 1966; Mendelson and Jennings, 1992; Waldron et al., 2006; Steen et al., 2007). Further details of these studies are provided in the sections that follow.

Space Use

Physical space represents the most basic of all resources. Space use is affected largely by the distribution of vital resources (food, shelter, and mates), predator-prey relationships, and especially in the case of reptiles, thermal constraints. Studies of space use have focused largely on characterizing space use in terms of home range size and microhabitat and macrohabitat selection. Such studies of snakes have documented species (Laurent and Kingsbury, 2003; Shine et al., 2003; Luiselli et al., 2007; Wasko and Sasa, 2010) and age- or sex-specific groups (Reinert, 1984; Roth, 2005; Blouin-Demers et al., 2007) using or selecting habitats out of proportion to their availability. Species-, age-, and sex-specific preferences highlight the potential for both intraspecific and interspecific habitat specialization within a given landscape.

In terms of interspecific space use, the manner in which sympatric species divide space directly relates to mechanisms of competition (Schoener, 1974), niche separation (Toft, 1985; Luiselli et al., 2006), and resource availability (Willson et al., 2006). Sympatric European *Vipera* partition space resources by occupying habitats at slightly different elevations (Brito and Crespo, 2002; Luiselli et al., 2007), whereas sympatric North American rattlesnakes (*Crotalus*) select macrohabitats differentially during the

active season (Pough, 1966; Mendelson and Jennings, 1992; Waldron et al., 2006; Steen et al., 2007). Additionally, the large sympatric vipers *Bitis gabonica* and *B. nasicornis* occupy different macrohabitats in Nigeria, to the degree that densities of the two species are inversely related (Luiselli, 2006).

Temporal Resources

Competitors frequently exhibit variable patterns of resource use in the presence of one another (Toft, 1985; Jones et al., 2001; Luiselli, 2003). In such settings, temporal partitioning of resources provides a platform for short- and long-term coexistence (Carother, 1984; Kotler et al., 1993; Kronfield-Schor and Dayan, 1999) while theoretically reducing interspecific competition (Toft, 1985; Martinez-Freiria et al., 2010). In addition to competition, predator avoidance (Kozlowski et al., 2008; Webb et al., 2009), physiological factors (Reinert, 1984; Huey, 1991; Roth, 2008), and environmental conditions (Wiest, 1981; Brito, 2003; Willson et al., 2006) also influence temporal use of resources. One of the best examples of temporal variation of resource use is that of anurans breeding in temporary ponds. Studies of sympatric anuran larva revealed that partitioning the timing of use of ponds was the single greatest measure of niche separation among sympatric tadpole species (Heyer, 1973; Wiest, 1981; Toft, 1985).

Many aspects of snake ecology are defined by temporal variation. Most notably, movements (Shine et al., 2003; Diffendorfer et al., 2005; Dugan et al., 2008), diet (Hartmann and Marques, 2005; Luiselli, 2003), foraging (Martins et al., 2002; Mori et al., 2002; Sun et al., 2001; Sorrell, 2009), and sexual activities (Shine and Madsen, 1997; Aldridge and Duvall, 2002; Schuett et al., 2005; Duvall et al., 1992) vary significantly

across daily, seasonal, and annual time frames. Martinez-Freiria et al. (2010), for example, noted temporal differences in the feeding periods, microhabitat use, and activity patterns of sympatric Mediterranean *Vipera* species in the Iberian Peninsula. The general plasticity of many snake traits (feeding, activity, and reproduction) and the ability to take advantage of temporally variable resources is just what has allowed for their successful radiation and survival in some of the most extreme environments on earth (Luiselli et al., 2002; Willson et al., 2006).

Thermal Resources

Reliance upon thermal resources is a critical aspect of the life history of ectothermic organisms. Many fundamental physiological processes, including food acquisition and digestion, locomotion, and reproduction, require microhabitats that provide sufficient opportunities to thermoregulate. Thermal gradients vary significantly both among and within habitat features of most macrohabitats. Understanding the interaction of thermal resource availability and behavior is vital to understanding the ecology of reptiles.

Lizards, particularly anoles (*Anolis* sp.), have featured extensively in studies of thermal biology as it relates to habitat and niche partitioning among sympatric species (Schoener and Gorman, 1968; Schettino et al., 2010). In their study of 11 sympatric *Anolis* species on Cuba, Schettino et al. (2010), for example, documented significant differences among the thermal environments occupied by the various species. Niche partitioning of the thermal, spatial, and temporal axes compensates for the speciose nature of that lizard community.

Unfortunately, studies of the thermal ecology of sympatric snakes lag far behind those of lizards. While many efforts have been made to characterize thermal resource use of individual snake species, few have examined more than a single species at a time. Intraspecific variation of thermal requirements is well documented among snakes, with gravid or pregnant females exhibiting unique patterns of temperature selection (Reinert, 1993; Charland, 1995; Gardner-Santana and Beaupre, 2009; Harvey and Weatherhead, 2010). While variation of thermal resource use within a species is largely related to reproductive condition, interspecific variation appears to be more complex. In terms of western rattlesnake species, thermal resources do not appear to play a vital role in structuring of sympatric populations. Beck (1995) found no differences in the body temperatures of active *Crotalus atrox*, *C. tigris*, and *C. molossus* inhabiting the Sonoran Desert of southern Arizona. Similarly, Pough (1966) did not detect a difference in temperatures at the time of collection of *C. atrox* and *C. scutulatus* along Portal Road in southeastern Arizona. However, in cooler environs where thermal resources are limited, partitioning along the thermal axis may play a greater role in both intraspecific and interspecific behavior (Reinert, 1984).

Diet

The evolution and biodiversity of snakes is strongly linked to the feeding ecology and general plasticity of their diets (Seigel, 1993). As top predators in nearly all ecosystems, understanding dietary preferences provides insight into behavior, predator-prey relationships, movements, habitat selection, and niche occupancy. Efforts to describe snake diets across a wide range of taxa have revealed non-random preferences, in terms of both prey composition and prey size (Holycross et al., 2002; Shetty and Shine,

2002; Halstead et al., 2008). It also appears that many snakes partition food resources in the presence of competitors (Toft, 1985; Luiselli, 2006). Feeding specialization and intraspecific niche shifts along the diet axis are generally interpreted as evolutionary responses to competition, often referred to as "the ghost of competition past" (Connell, 1980). Among species within the same feeding guild, niche shifts ultimately serve to reduce competition and provide increased fitness via mechanisms of niche partitioning. Therefore, efforts to characterize interspecific niche partitioning along the diet axis should focus on closely related species within the same feeding guild.

Studies of snake diet are plentiful and have focused on diverse taxa from across the globe. The resulting body of literature has yielded significant knowledge about how snakes find and secure prey, and how diets relate to the overall ecology of snakes. Among snakes, sympatric vipers frequently occupy similar fundamental niches and provide ideal opportunities to use comparative approaches to examine diet. A review of the literature reveals that many snake species exhibit intraspecific variation, with differences among age classes (e.g., Mackessy, 1988; Taylor, 2001; Avila-Villegas et al., 2007; Lin and Tu, 2008) and sexes (e.g., Houston and Shine, 1993; Daltry et al., 1998; Shetty and Shine, 2002; Glaudas et al., 2008; Lin and Tu, 2008) being common. Among vipers, sexual differences are more unusual than ontogenetic differences; prior to our work (Dugan and Hayes, under review; Chapter 4), for example, none had been found among rattlesnakes. Although some wide-ranging species show little geographic variation in diet (Spencer, 2003), most species exhibit significant variation across their range (Daltry et al., 1998; Clark, 2002; Creer et al., 2002; Santos et al., 2008; Dugan and Hayes, in review). In addition, some viper diets exhibit seasonal variation (Holycross et

al., 2002; Glaudas et al., 2008; Santos et al., 2008), with prey availability suggested as a causal factor.

Although snake diets have been well-studied, dietary information regarding interspecific variation between and among sympatric vipers, and western vipers in particular, is nearly non-existent. What little has been written stems largely from the work of Luca Luiselli and his colleagues. Luiselli et al. (2007) recorded significantly different diets among two sympatric species of *Vipera* in Italy. Conversely, diets of sympatric *Bitis* species were largely similar in southern Nigeria (Luiselli and Akani, 2003). In North America, dietary differences clearly exist among sympatric species of very different body sizes (e.g., *C. atrox* versus *C. cerastes* in southwestern deserts; *C. adamanteus* versus *Sistrurus miliarius* in southeastern forests; Klauber, 1972), but the extent of differences among those of similar body size warrants closer scrutiny. Dietary differences could result from either prey preference or differential habitat use, since prey availability also differs among habitats. Several studies have demonstrated that snakes opportunistically consume prey species available in the habitats they occupy (Reynolds and Scott, 1982; Hirai, 2004; Hartmann and Marques, 2005). Thus, distinguishing between habitat use and diet as a basis for niche partitioning can prove difficult.

Niche Partitioning by Red Diamond and Southern Pacific Rattlesnakes

The purpose of my studies was to detail and compare resource use and niche partitioning among sympatric populations of the red diamond rattlesnake (*C. ruber*) and southern Pacific Rattlesnake (*C. oreganus helleri*) in southern California. Efforts to examine resource partitioning among vipers, particularly North American vipers, are

surprisingly scant in the literature (Toft, 1985; Luiselli, 2006). In conducting these studies, I sought to fill this void.

In **Chapter 2**, I compare the home range size, movements, and mating phenology of sympatric *C. ruber* and *C. o. helleri* in Chino Hills State Park. In this study, I consider two measurements of space use: home range size and mean daily movement. I compared home range size across species and seasons (two active seasons and one winter) using both minimum convex polygons (MCP) and fixed-kernel (FK) home range estimators. Mean daily movements were assessed at three temporal levels: daily, monthly, and seasonal. The phenology (seasonal timing) of sexual activities was also compared between the two species. I discuss results in the context of competitive mechanisms and niche partitioning.

In **Chapter 3**, I provide the single most extensive examination of comparative resource use among sympatric North American vipers to date. In this study, I compared the rattlesnakes *C. ruber* and *C. o. helleri* along all four major niche axes (space, temporal, diet, thermal) using radio-telemetry and mark-recapture data collected from my Chino Hills State Park study site.

Spatial resources were analyzed in terms of both macrohabitat and microhabitat. I identified five major macrohabitats at the site: cactus, coastal sage-scrub (CSS), non-native grassland, riparian, and oak woodland (Sampson, 1985). Analysis of macrohabitat use involved both compositional analysis (Aebischer et al., 1993) and logistic regression (Mertler and Vannatta, 2004). Microhabitat use (underground, above-ground, or arboreal) was also considered in terms of underground, aboveground, and arboreal use.

Thermal resources were analyzed using three temperature measurements (ambient air, ground in the shade, ground in the sun) taken at each fix when the snake was above-ground. I also compared the three temperature measurements among the five macrohabitats to address potential differences of thermal resource availability.

I further evaluated species differences in temporal resource use. Activity (immobile, locomoting, or sexual) was considered in terms of frequency, and seasonal differences in activity was examined across three periods (spring, summer, and fall) of the active season. Circadian activity was also assessed during the active season.

I examined use of dietary resources via scat samples and feeding observations procured in the field. Dietary data were used to investigate the following three hypotheses: (1) The two species differ in proportions of prey genera consumed; (2) Differences in diet composition corresponds to differences in preferred habitat of the snakes, and (3) Based on a larger gape size, *C. ruber* consumes larger prey species more often than *C. o. helleri*.

I calculated interspecific niche overlap using the symmetric formulas of Pianka and Czekanowski niche overlap indices. Overlap indices were obtained for all of the major niche axes, including macrohabitat use, microhabitat use, thermal resources, seasonal and circadian movements, and food type and size. I then used null models to test whether niche overlap values were significantly less than expected by chance.

In **Chapter 4**, I provide a detailed description of the diet of the red diamond rattlesnake (*C. ruber*). The diet of *C. o. helleri* was studied in detail previously (Mackessy, 1988), but no comparable study had been undertaken for *C. ruber*. Samples were obtained from museum specimens, fecal samples from live specimens at my study

site, opportunistic field observations, published accounts, and data collected from road-killed specimens. Dietary data for *C. ruber* were collected from across the species' range, including southern California (USA) and Baja Norte and Baja Sur (Mexico). Thus, the rangewide description allowed for broader comparisons with *C. o. helleri* that extended beyond my study site. Intraspecific variation of diet was analyzed in terms of ontogenetic change and sexual and geographic differences.

In *Chapter 5*, I draw general conclusions from my research and discuss the findings in the context of current theory.

References

- ADLER, P. B., J. HILLE RIS LAMBERS, AND J. M. LEVINE. 2007. A niche for neutrality. *Ecology Letters* 10:95–104.
- AEBISCHER, N. J., P. A. ROBERTSON, AND R. E. KENWARD. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313–1325.
- ALDRIDGE, R. D. AND D. DUVALL. 2002. The evolution of mating seasons in the pitvipers of North America. *Herpetological Monographs* 16:1–25.
- BLOUIN-DEMERS, G., L. P. G. BJORGAN, AND P. J. WEATHERHEAD. 2007. Changes in habitat use and movement patterns with body size in black ratsnakes (*Elaphe obsoleta*). *Herpetologica* 63:421–429.
- BRITO, J. C., AND E. G. CRESPO. 2002. Distributional analysis of two vipers (*Vipera latastei* and *V. seoanei*) in a potential area of sympatry in the northwestern Iberian Peninsula. Pp. 129–138 in G. W. Schuett, M. Höggren, M. E. Douglas, and H. W. Greene (eds.), *Biology of the Vipers*. Eagle Mountain Publishing, Eagle Mountain, Utah.
- BRITO, J. C. 2003. Seasonal variation in movements, home range, and habitat use by male *Vipera latastei* in northern Portugal. *Journal of Herpetology* 37:155–160.
- CADOTTE, M. W. 2007. Concurrent niche and neutral processes in the competition-colonization model of species coexistence. *Proceedings of the Royal Society B* 274:2739–2744.
- CAROTHERS, J. H. 1984. Time as a niche difference: the role of interference competition. *Oikos* 42:403–406.
- CHARLAND, M. B. 1995. Thermal consequences of reptilian viviparity: thermoregulation in gravid and nongravid garter snakes (*Thamnophis*). *Journal of Herpetology* 29:383–390.
- CHESSON, P. 2000. Mechanism of maintenance of species diversity. *Annual Review of the Ecology and Systematics* 31:343–366.
- CONNELL, J.H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35, 131–138.
- DIFFENDORFER, J. E., C. ROCHESTER, R. N. FISHER, AND T. K. BROWN. 2005. Movement and space use by coastal rosy boas (*Lichanura trivirgata roseofusca*) in coastal Southern California. *Journal of Herpetology* 39:24–36.

- DUELLMAN, W. E. 1990. Herpetofaunas in neotropical rainforests: Comparative composition, history, and resource use. Pp. 455–486. In: Gentry A. H. (ed.), *Four Neotropical Rainforests*. Vail-Ballou Press, Binghamton, New York, USA.
- DUGAN, E. A., AND W. K. HAYES. In review. Diet and feeding ecology of the red diamond rattlesnake, *Crotalus ruber* (Serpentes: *Viperidae*).
- DUVALL, D., S. J. ARNOLD, AND G. W. SCHUETT. 1992. Pitviper mating systems: ecological potential, sexual selection, and microevolution. Pp. 169–184 *In* J. A. Campbell and E. D. Brodie Jr. (eds). *Biology of the Pitvipers*. Selva Press, Tyler, Texas.
- FEINSINGER, P., E. E. SPEARS, AND R. W. POOLE. 1981. A simple measure of niche overlap. *Ecology* 62:27–32.
- GARDNER-SANTANA, L. C. AND S. J. BEAUPRE. 2009. Timber rattlesnakes (*Crotalus horridus*) exhibit elevated and less variable body temperatures during pregnancy. *Copeia* 2009:363–368.
- GOODYEAR, S. E., AND E. R. PIANKA. 2008. Sympatric ecology of five species of fossorial snakes (*Elapidae*) in western Australia. *Journal of Herpetology* 42:279–285.
- GRANT, P. R. AND B. R. GRANT. 2006. Evolution of character displacement in Darwin's finches. *Science* 313:224–226.
- GREGORY, P. T., J. M. MACARTNEY, AND K. W. LARSEN. 1987. Spatial patterns and movements. Pp. 366–395 *in* R. A. Seigel, J. T. Collins, and S. S. Novak (eds.), *Snakes: Ecology and Evolutionary Biology*. McGraw-Hill, Inc., New York, New York.
- HARTMANN, P. A., AND A. V. MARQUES. 2005. Diet and habitat use of two sympatric species of *Philodryas* (*Colubridae*), in south Brazil. *Amphibia-Reptilia* 26:25–31.
- HARVEY, D. S. AND P. J. WEATHERHEAD. 2010. Habitat selection as the mechanism for thermoregulation in a northern population of massasauga rattlesnakes (*Sistrurus catenatus*). *Ecoscience* 17:411–419.
- HIRAI, T. 2004. Dietary shifts of frog eating snakes in response to seasonal changes in prey availability. *Journal of Herpetology* 38:455–460.
- HOUSTON D. L., AND R. SHINE. 1993. Sexual dimorphism and niche divergence: feeding habits of the arafura file snake. *Journal of Animal Ecology* 62:737–749.
- HUBBELL, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Monographs in Population Biology. Princeton, NJ: Princeton University Press.

- HUBBELL, S. P. 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology* 19:166–172.
- HUEY, R. B. 1991. Physiological consequences of habitat selection. *American Naturalist* 137:91–115.
- HURTT, G. C. AND S. W. PACALA. 1995. The consequences of recruitment limitation. Reconciling chance, history, and competitive differences between plants. *Journal of Theoretical Biology* 176:1–12.
- JONES, M., Y. MANDELIK, AND T. DAYAN. 2001. Coexistence of temporally partitioned spiny mice: roles of habitat structure and foraging behavior. *Ecology* 82:2164–2176.
- KRONFIELD-SCHOR, N. AND T. DAYAN. 1999. The dietary basis for temporal partitioning: food habits of coexisting *Acomys* species. *Oecologia* 121:123–128.
- KOTLER, B. P., J. S. BROWN, AND A. SUBACH. 2003. Mechanisms of species coexistence of optimal foragers: temporal partitioning by two species of sand dune gerbils. *Oikos* 67:548–556.
- LAURENT E. J. AND B. A. KINGSBURY. 2003. Habitat separation among three species of water snake in northwestern Kentucky. *Journal of Herpetology* 37:229–235.
- LIN, C. F. AND M. C. TU. 2008. Food habits of the Taiwanese mountain pitviper, *Trimeresurus gracilis*. *Zoological Studies* 47:697–703.
- LUISELLI, L. 2003. Do snakes exhibit shifts in feeding ecology associated with the presence or absence of potential competitors? A case study from tropical Arica. *Canadian Journal of Zoology* 81:228–236.
- LUISELLI, L., AND F. M. ANGELICI. 2000. Ecological relationships in two Afrotropical cobra species (*Naja melanoleuca* and *Naja nigricollis*). *Canadian Journal of Zoology* 78:191–198.
- LUISELLI, L., AND G. C. AKANI. 2003. Diet of sympatric gaboon vipers (*Bitis gabonica*) and nose-horned vipers (*Bitis nasicornis*) in southern Nigeria. *African Journal of Herpetology* 52:101–106.
- LUISELLI, L., G. C. AKANI, AND D. CAPIZZI. 1998. Food resource partitioning of a community of snakes in a swamp rainforest of south-eastern Nigeria. *Journal of Zoology* 246:125–133.
- LUISELLI, L., F. M. ANGELICI, AND G. C. AKANI. 2002. Comparative feeding strategies and dietary plasticity of the sympatric cobras *Naja melanoleuca* and *Naja*

- nigricollis* in three diverging Afrotropical habitats. Canadian Journal of Zoology 80:55–63.
- MACKESSY, S. P. 1988. Venom ontogeny in the Pacific rattlesnakes *Crotalus viridis helleri* and *C. v. oreganus*. Copeia 1988:92–101.
- MARTINEZ-FREIRIA, F., M. LIZANA, J. P. DO AMARAL, AND J. C. BRITO. 2010. Spatial and temporal segregation allows coexistence in a hybrid zone among two Mediterranean vipers (*Vipera aspis* and *V. latastei*). Amphibia-Reptilia 31:195–212.
- MARTINS, M., O. V. MARQUES, AND I. SAZIMA. 2002. Ecological and phylogenetic correlates of feeding habits in neotropical pitvipers of the genus *Bothrops*. Pp. 307–328 in G. W. Schuett, M. Höggren, M. E. Douglas, and H. W. Greene (eds.), Biology of the Vipers. Eagle Mountain Publishing, Eagle Mountain, Utah.
- M'CLOSKEY, R. T. (1978) Niche separation and assembly in four species of Sonoran Desert rodents. American Naturalist 112:683–694.
- MERTLER, C. A., AND R. A. VANNATTA. 2004. Advanced and Multivariate Statistical Methods: Practical Application and Interpretation. 3rd Edition. Pyrczak Publishing, Los Angeles, California, USA.
- METZGER, C. S. URSENBACHER, AND P. CHRISTE. 2009. Testing the competitive exclusion principle using various niche parameters in a native (*Natrix maura*) and introduced (*N. tessellata*) colubrid. Amphibia-Reptilia 30:523–531.
- MORI, A., M. TODA, AND H. OTA. 2002. Winter activity of the hime-habu (*Ovophis okinavensis*). Pp. 329–344 in G. W. Schuett, M. Höggren, M. E. Douglas, and H. W. Greene, Biology of the Vipers (eds.). Eagle Mountain Publishing, Eagle Mountain, Utah.
- PFENNIG, D. W., A. M. RICE, AND R. A. MARTIN. 2006. Ecological opportunity and plasticity interaction to promote character displacement and species coexistence. Ecology 87:769–779.
- PIANKA, E. R. 1974. Niche overlap and diffuse competition. Proceedings of the National Academy of Sciences 71:2141–2145.
- PIANKA, E. R. 1981. Competition and niche theory. Pp. 167–196 in R. May (ed.), Theoretical Ecology. Principles and Applications. Blackwell, Oxford, United Kingdom.
- REINERT, H. K. 1984. Habitat variation within sympatric snake populations. Ecology 65:1673–1682.

- RICCIARDI, A., R. J. NEVES, AND J. B. RASMUSSEN. 1998. Impending extinctions of North American freshwater mussels (Unionoida) following the zebra mussel (*Dreissena polymorpha*) invasion. *Journal of Animal Ecology* 67:613–619.
- ROTH, E. D. 2005. Buffer zone application in snake ecology: a case study using cottonmouths (*Agkistrodon piscivorus*). *Copeia* 399–402.
- SAMPSON, G. T. 1985. The flora of Chino Hills State Park. M.A. Thesis, California State University, Fullerton, USA.
- SANTOS, X., J. BRITO, N. SILLERO, J. M. PLEGUEZUELOS, G. LLORENTE, S. FAHD, AND X. PARELLADA. 2006. Inferring habitat-suitability areas with ecological modeling techniques and GIS: A contribution to assess the conservation status of *Vipera latastei*. *Biological Conservation* 130:416–425.
- SANTOS, X., J. M. PLEGUEZUELOS, J. C. BRITO, G. A. LLORENTE, X. PARELLADA, AND S. FAHD. 2008. Prey availability drives geographic dietary differences of a Mediterranean predator, the lataste's viper (*Vipera latastei*). *Herpetological Journal* 18:16–22.
- SCHOENER, T. W. 1974. Resource partitioning in ecological communities. *Science* 185:27–39.
- SCHUETT, G. W., D. L. HARDY, H. W. GREENE, R. L. EARLEY, M. S. GROBER, E. A. VAN KIRK, AND W. J. MURDOCH. 2005. Sympatric rattlesnakes with contrasting mating systems show differences in seasonal patterns of plasma sex steroids. *Animal Behavior* 70:257–266.
- SHETTY, S., AND R. SHINE. 2002. Sexual divergence in diets and morphology in Fijian sea snakes *Laticauda colubrina* (Laticaudinae). *Austral Ecology* 27:77–84.
- SHINE, R. A., AND T. MADSEN. 1997. Prey abundance and predator reproduction: Rats and pythons on a tropical Australian floodplain. *Ecology* 78:1078–1086.
- SHINE, R., AND X. BONNET. 2000. Snakes: a new “model organism” in ecological research? *Trends in Ecology and Evolution* 15:221–222.
- SHINE, R. A., T. SHINE, AND B. SHINE. 2003. Intraspecific habitat partitioning by the sea snake *Emydocephalus annulatus* (Serpentes, Hydrophiidae): The effects of sex, body size, and colour pattern. *Biological Journal of the Linnean Society* 80:1–10.
- SHINE, R., L. SUN, M. FITZGERALD, AND M. KEARNEY. 2003. A radiotelemetric study of movements and thermal biology of insular Chinese pit-vipers (*Gloydius shedaoensis*, Viperidae). *Oikos* 100:342–352.

- SORRELL, G. G. 2009. Diel movement and predation activity patterns of the eyelash palm-pitviper (*Bothriechis schlegelii*). *Copeia* 2009:105–109.
- SPENCER, C. L. 2003. Geographic variation in the morphology, diet and reproduction of a widespread pitviper, *Crotalus atrox*. Ph.D. Dissertation, University of Texas at Arlington, Arlington, Texas.
- SUN, L., R. SHINE, Z. DEBI, AND T. ZHENGREN. 2001. Biotic and abiotic influence on activity patterns of insular pit-vipers (*Gloydius shedaoensis*, Viperidae) from north-eastern China. *Biological Conservation* 97:387–398.
- VANDERMEER, J. H. 1972. Niche theory. *Annual Review of Ecology and Systematics* 3:107–132.
- VERGNON, R., N. K. DULVY, AND R. P. FRECKLETON. 2009. Niches versus neutrality: Uncovering the drivers of diversity in a species-rich community. *Ecology Letters* 12:1079–1090.
- WASKO, D. K., AND M. SASA. 2009. Activity patterns of a neotropical ambush predator: spatial ecology of the fer-de-lance (*Bothrops asper*, Serpentes: Viperidae) in Costa Rica. *Biotropica* 41:241–249.
- WASKO, D. K., AND M. SASA. 2010. Habitat selection of the terciopelo (Serpentes: Viperidae: *Bothrops asper*) in lowland rainforest in Costa Rica. *Herpetologica* 66:148–158.
- WEBB, J. K., R. M. PRINGLE, AND R. SHINE. 2009. Intraguild predation, thermoregulation, and microhabitat selection by snakes. *Behavioral Ecology* 20:271–277.
- WIEST, J. A. JR. 1981. Anuran succession at temporary ponds in post oak savanna region of Texas. Pp. 39–47 in N. J. Scott (ed), *Herpetological Communities*. U.S. Department of the Interior, Fish and Wildlife Service. Wildlife Research Report 13.
- WILLSON, J. D., C. T. WINNE, M. E. DORCAS, AND J. W. GIBBONS. 2006. Post-drought responses of semi-aquatic snakes inhabiting an isolated wetland: insights on different strategies for persistence in a dynamic habitat. *Wetlands* 26:1071–1078.

CHAPTER TWO
HOME RANGE SIZE, MOVEMENTS, AND MATING PHENOLOGY
OF SYMPATRIC RED DIAMOND (*CROTALUS RUBER*) AND
SOUTHERN PACIFIC (*C. OREGANUS HELLERI*) RATTLESNAKES
IN SOUTHERN CALIFORNIA

ERIC A. DUGAN¹, ALEX FIGUEROA¹, AND WILLIAM K. HAYES¹

¹*Department of Earth and Biological Sciences, Loma Linda University,
Loma Linda, California 92350 USA*

This chapter has been published with the following citation:

DUGAN, E. A., A. FIGUEROA, AND W. K. HAYES. 2008. Pp. 353–364 in W. K. Hayes, K. R. Beaman, M. D. Cardwell, and S. P. Bush (eds.), *The Biology of Rattlesnakes*. Loma Linda University Press, Loma Linda, California.

Abstract

Although many sympatric snake species partition food to reduce interspecific competition, rattlesnakes and other vipers, like most vertebrates, typically partition the habitat. To evaluate this generality, we used radiotelemetry to study the home range sizes, movements, and mating phenology of sympatric adult male red diamond (*Crotalus ruber*) and southern Pacific (*C. oreganus helleri*) Rattlesnakes in a coastal valley of southern California. Mean home range sizes and mean daily movements were substantially greater in *C. ruber* than in *C. o. helleri*. Both species occupied much larger home ranges during the two active seasons (March-November) compared to the winter season. Mating seasons differed between the two species, with *C. ruber* engaging in accompaniment, courtship, and copulation exclusively in the spring and *C. o. helleri* exhibiting reproductive behavior during both late summer/fall and spring. Annual movements by *C. o. helleri* spiked in both spring and late summer/fall, whereas movements of *C. ruber* spiked also in spring but less dramatically in late summer/fall. Spatial use and movement differences between the two species likely resulted from distribution of preferred habitat at the study site (limited *Opuntia* cactus patches for *C. ruber*, widespread non-native grassland and riparian habitats for *C. o. helleri*) and differences in mating phenology (*C. o. helleri* males searching for mates in two seasons versus one for *C. ruber*). Thus, these two species, like other sympatric rattlesnakes and vipers studied to date, appear to partition habitat. However, unlike other sympatric rattlesnakes studied to date, *C. ruber* and *C. o. helleri* also differ in their use of spatial and temporal resources, though probably not as a direct result of competitive mechanisms.

Introduction

Niche Theory predicts that closely-related sympatric species should partition resources to avoid or reduce interspecific competition (Pianka, 1981; Walter, 1991). Niche separation can be achieved via differences in food (type or size) or in use of spatial (macrohabitat or microhabitat), temporal (diel or seasonal activity patterns), or thermal resources (Saint Girons, 1978; Schoener, 1974). Snakes have been considered atypical among vertebrates because sympatric species usually partition food rather than habitat (Luiselli, 2006a; Toft, 1985; Vitt, 1987;). However, sympatric viper species apparently adhere to the typical vertebrate pattern, primarily partitioning habitat (Luiselli, 2006a,b; Luiselli et al., 2007).

Rattlesnakes (genera *Crotalus* and *Sistrurus*) represent an ideal group for exploring niche separation in vipers. The ranges of many species often overlap broadly, particularly in the arid and semi-arid regions of southwest North America, where species richness is highest (Beaman and Hayes, this volume; Klauber, 1972;). The few studies of this group support the view that sympatric rattlesnake species primarily partition habitat. Pough (1966), Reynolds and Scott (1982), and Mendelson and Jennings (1992) demonstrated differences in habitat use of *Crotalus atrox*, *C. molossus*, and *C. scutulatus* in the Sonoran Desert of southeast Arizona, southwest New Mexico, and northern Chihuahua, Mexico. Beck (1995) determined that sympatric *C. atrox*, *C. molossus*, and *C. tigris* in southeast Arizona use different habitats, but otherwise exhibit similar home range sizes, activity patterns, thermal ecology, and annual food intake. Waldron et al. (2006b) found that sympatric *C. adamanteus* and *C. horridus* in coastal South Carolina prefer different habitats, but occupy similar home range sizes. Steen et al. (2007) also

showed that sympatric *C. adamanteus* and *C. horridus* in coastal Georgia use different habitats. Reinert (1984) determined that *C. horridus* and another sympatric viper, *Agkistrodon contortrix mokeson*, prefer different habitats in eastern Pennsylvania.

Differences in space use and movements by sympatric rattlesnakes could be expected for many reasons apart from competitive mechanisms. The distribution and abundance of critical resources greatly influence the movement patterns of snakes (Gregory et al., 1987). Critical resources for rattlesnakes include required habitat, food, access to potential mates, protection from predators, and suitable thermoregulation and overwintering sites (e.g., Duvall and Schuett, 1997; Reinert and Zappalorti, 1988; Secor, 1992). Temporal variation in resources and needs also influences movements by snakes (Seigel and Pilgrim, 2002). Some crotaline snakes, for example, mate only in spring, some mate only in late summer/fall, and others exhibit a bimodal mating phenology, with copulations occurring during both late summer/fall and spring (i.e., interrupted by hibernation; Aldridge and Duvall, 2002; Schuett et al., 2002). During mating season, males frequently undertake extensive searches for mates (e.g., Aldridge and Brown, 1995; Ashton, 2003; Brown et al., this volume; Cardwell, 2008; Duvall et al., 1992; Goode et al., this volume; Jellen et al., 2007; Marshall et al., 2006; Prival et al., 2002; Sealy, 2002; Secor, 1992; Waldron et al., 2006a). Rattlesnake activity also shifts dramatically with seasonal changes in temperature and rainfall (e.g., Goode et al., this volume; Prival et al., 2002). Thus, differences in space use and movements by sympatric rattlesnakes could result from differences in preferred habitats and species-specific eco-physiological constraints.

The red diamond rattlesnake (*C. ruber*) is a large-bodied pitviper distributed from southern California southward throughout the Baja peninsula and several of its associated islands (Grismer, 2002). *Crotalus ruber* can be found from the desert slopes to the coastline, and preys predominately on rodents (Dugan, unpubl. data; Klauber, 1972). The red diamond rattlesnake is currently listed as a species of special concern by the State of California (Jennings and Hayes, 1994). To date, no published accounts exist detailing the biology of this species (Beaman and Dugan, 2006); however, recent research has begun to address this void in our knowledge (Brown et al, this volume; Greenberg, 2002; Halama et al., this volume).

The southern Pacific rattlesnake (*C. oreganus helleri*; Ashton and De Queiroz, 2001) is another large-bodied pitviper, distributed from central California southward into northern Baja (Grismer, 2002). This snake is considered a habitat generalist (Stebbins, 2003), as it inhabits a wide range of habitats from montane coniferous forests to coastal sage scrub along the coast. The western rattlesnake complex (*C. viridis* + *C. oreganus* + *C. cerberus*) is one of the most extensively studied group of snakes (Beaman and Hayes, this volume; Diller and Wallace, 2002). However, no quantitative data have been published on movements and habitat use of *C. o. helleri*.

The close phylogenetic relationship and extensive overlap of the ranges, habitat, and general life histories makes these two species ideal candidates for studies of niche separation and interspecific variation in natural history. In California, coastal populations of both species coexist in a rapidly-fragmenting environment, placing many remaining populations in danger of genetic isolation and local extirpation (Halama et al., this volume). Accordingly, we need a better understanding of the ecology of these two

broadly sympatric species, not just for behavioral and ecological theory, but also for conservation concerns. The data presented herein address the following questions as they relate to potential niche separation. 1) Do home ranges of sympatric *C. ruber* and *C. o. helleri* differ in area and by season? 2) Do movements of sympatric *C. ruber* and *C. o. helleri* differ in magnitude and by season? And finally, 3) does the phenology of reproductive activity differ between *C. ruber* and *C. o. helleri*? Additional data collected during this study on habitat use, diet, and survival will be presented in a separate manuscript.

Materials and Methods

Study Site

The study site encompassed ca. 30 ha in the southeastern portion of Chino Hills State Park (CHSP), California (33E54' N, 117E42' W). A north-south running canyon with a small semi-perennial creek dominates the site's topography. The CHSP system comprises ca. 5,039 ha in Los Angeles, Orange, Riverside, and San Bernardino counties, and ranges in elevation from 131 to 543 m (Keller, 1992; Goodman, 1997; http://www.stateparks.com/chino_hills.html).

We identified five major habitats at the study site: cactus, coastal sage scrub (CSS), non-native grassland, riparian, and oak woodland. Cactus patches of coastal pricklypear (*Opuntia littoralis*) were found exclusively on south-facing slopes and represented the habitat with the smallest distribution at our site. The distribution of CSS was patchy, primarily on south-facing slopes. Non-native grassland was the most widespread, occurring on both hillsides and in canyon bottoms. The riparian system was largely confined to the creek channel, but penetrated into damper drainages of the

grassland. Oak woodland was found primarily on north-facing slopes, but was not used by any of the telemetered snakes in this study. The study site was devoid of rock outcroppings, as the soil is predominately clay. Sampson (1985) provides further details on relative abundance and species composition of these plant communities.

The site experiences a Mediterranean climate. Average annual precipitation ranges from 35–46 cm, with the majority of rainfall occurring during the winter and spring months (Sampson, 1985). Winters are mild (average daily low in January = 5.6°C) and summers hot and dry (average daily high in July = 31.7 °C), with temperatures occasionally exceeding 38°C.

Radio-Telemetry

We began collecting, marking, and implanting snakes with radio-transmitters in March 2003. Individuals were tracked from March 2003 through December 2004. Visual searches and road surveys were used to obtain snakes of both species. Snakes were anesthetized with sevoflurane (Halocarbon Products Corp., River Edge, New Jersey, USA) while restrained within clear plastic tubes (Hardy and Greene, 1999) to allow collection of various measurement data. We recorded snout-vent length (SVL), total length, mass, rattle number, number of subcaudal scales, and sex for each snake. Adult snakes were sexed using Neosporin-lubricated sexing probes. All individuals were marked with a passive integrative transponder (PIT) tag (AVID Identification Systems, Inc., Norco, California, USA). PIT tags allowed us to permanently identify individuals as part of a long-term mark-recapture effort.

We used SI-2T temperature-sensitive transmitters (Holohil Systems Ltd., Ontario, Canada) to monitor up to six males of each species simultaneously. Transmitters weighed

9 g and always represented <5% of an individual's body mass (Hardy and Greene, 1999). Surgical procedures followed the guidelines and methods described by Reinert and Cundall (1982) and Hardy and Greene (1999). Snakes were released at their collection site 24–36 hr post-surgery. Minimizing time in captivity has been shown to increase post-surgical survival (Hardy and Greene, 1999). Sampling effort varied seasonally as snake activity patterns changed. Individuals were located 1–4 times/wk throughout the active season (March–November) and less often (bi-monthly) during the winter period (December–February). Telemetered snakes were relocated using a Telonics TR2 receiver (Telonics, Mesa, Arizona, USA) and a hand-held four-element yagi antenna. Upon each relocation, we visually located each snake if possible and recorded the universal transverse mercator (UTM) coordinates with a handheld GPS unit (Garmin GPS Plus III; Garmin Ltd., George Town, Cayman Islands). When snakes were located in dense, impenetrable cactus patches, coordinates were taken at the closest location possible (within 5 m of presumed location).

Data presented herein were collected from nine adult male *C. o. helleri* (84–103 cm SVL) and seven adult male *C. ruber* (98–156 cm SVL). Snakes were lost (predation, transmitter battery failure) or added opportunistically throughout the study, resulting in variable tracking periods (202–905 d) for different individuals.

Home Range Size and Movements

Based on location data, we computed two estimates of home range size, one estimate for autocorrelation, and one movement variable (see below). We compared each of these dependent measures for the two species and for three seasons: active season

(March–November) 2003, winter season (December–February) 2003–2004, and active season (March–November) 2004.

We computed seasonal home range sizes using both minimum convex polygons (MCP) and fixed-kernel (FK) methods. We used Calhome 1.0 (Kie et al., 1994) and HomeRanger 1.5 (Hovey, 1999) to obtain 100% MCP and 95% FK, respectively. We used all fixes obtained from each individual for our analyses and software defaults, including least-squares cross-validation as the smoothing factor for FK. Although FK estimates are increasingly preferred (Powell, 2000), MCP estimates continue to be reported and are more available in the literature for comparisons between studies. Both estimates are sensitive to sample size, with MCP increasing asymptotically and FK decreasing asymptotically with increasing number of fixes (Seaman et al., 1999). Opinions remain contentious as to which estimate (MCP vs. FK) performs better (e.g., Row and Blouin-Demers, 2006; Laver and Kelly, 2008). HomeRanger also computed autocorrelation (t^2/r^2) for each snake, a measure of temporal independence between successive fixes. When autocorrelation exists ($t^2/r^2 < 2$), the distance moved between consecutive observations decreases, resulting in underestimates of FK (Swihart and Slade, 1985).

We considered movements at three time levels: daily, monthly, and seasonal. We used the mean distance moved per day as our fundamental unit of measurement for individual snakes. This was computed from the distance moved between each two consecutive fixes divided by the number of days between the two fixes (Gregory et al., 1987). To obtain mean daily movements per month, we calculated the mean of all such measurements procured within a given month for each snake. To avoid bias from uneven

sampling across months, mean daily movements per season were computed as the average of all monthly estimates (rather than the mean from all fixes) for those months within a given season.

Mating Phenology

Data were collected opportunistically from both telemetered and non-telemetered snakes throughout the duration of the study. We recorded two types of sexual activities: accompaniment (pairs coiled next to or within 0.5 m of each other, often with males chin-rubbing and/or pursuing females in courtship; c.f. Duvall et al., 1992; Duvall and Schuett, 1997) and copulations. Non-sexual accompaniment during the winter months (overwintering at same site, November–February) was excluded. We also gleaned additional observations from the existing literature on *C. ruber* and *C. o. helleri*.

Statistical Analyses

Our primary interest was to examine the effects of species and season on spatial use and movements. For home range and movement data, we subjected each of the four dependent variables (100% MCP and 95% FK estimates of home range size, mean daily movements, and autocorrelation values) to three analyses.

First, to evaluate species and season simultaneously, we conducted 2×3 analyses of variance (ANOVAs; Mertler and Vannatta, 2004), treating species (two levels) as a between-subjects factor and season (three levels) as a within-subjects factor. Because some telemetered snakes were lost during the study (one of the initial six *C. ruber* became ill; three of the initial six *C. o. helleri* were predated) and then replaced by others, only five *C. ruber* and three *C. o. helleri* were tracked continuously over the three

seasons, rendering a small sample size. Effect sizes from the ANOVAs were obtained as partial η^2 values (Cohen, 1988), indicating the approximate proportion of variance in the dependent variable explained by each independent variable or interaction, with values >0.25 generally considered large. When multiple effect sizes within a model summed to >1 , we adjusted the values by dividing each partial η^2 by the sum of all partial η^2 values. Second, we conducted independent-samples *t*-tests to compare the two species for each of the three seasons, and computed Cohen's *d* (Cohen, 1988) for effect sizes using pooled standard deviation. Cohen's *d* values >0.8 are generally considered large effects. This within-season paired-comparison approach utilized all of the available subjects, increasing the sample size for the two active seasons ($n = 6$ for each species). Third, we used Pearson correlation coefficients to examine associations among the home range estimators (MCP and FK), number of fixes, autocorrelation, and movements.

Data used in these analyses were examined to determine whether parametric assumptions were met, and the fit was found to be acceptable in all cases. We also conducted non-parametric equivalents of *t*-tests and Pearson coefficients, but because the conclusions were identical, we report only the parametric outcomes.

Frequency data for sexual behavior were compared between the two species for the spring and late summer/fall seasons. The resulting 2×2 contingency table had too few cells with expected frequency ≥ 5 to use Chi-square tests. Thus, we evaluated the strength of asymmetry between species and seasons using Cramer's *V* (Conover, 1999).

Analyses were conducted using SPSS 12.0 for Windows (SPSS, 2003) with alpha set at 0.05.

Results

Home Range Size

The two estimates of home range size (100% MCP and 95% FK) are summarized in Table 2-1 for each snake during each of the three seasons (the FK estimate for CR2 in the active season 2004 was deleted from analysis as an obvious outlier). Individual home range estimates varied from 0.15–23.02 ha during the active season and from 0.01–0.26 ha during the winter. Comparisons between species and seasons are depicted in Fig. 2-1. The main effect of species in the ANOVA model was not significant for either MCP or FK (both $P \geq 0.16$ and partial $\eta^2 \leq 0.32$; Table 2-2). However, the main effect of season was significant for both MCP and FK ($P = 0.041$ and 0.033 , respectively), with each measure having a large effect size (partial $\eta^2 = 0.47$ and 0.43 , respectively; Table 2-2). As expected, the snakes occupied much smaller home ranges during the winter, with *C. ruber* and *C. o. helleri* averaging 3.6% and 1.8% of their active-season home ranges, respectively (computed using species means in Table 2-1, with active-season home range calculated as the average for the two estimators, and averaged again for the two active seasons). No interactions between season and species were detected (both $P > 0.20$ and partial $\eta^2 = 0.25$; Table 2-2). Given the relatively large effect sizes (Cohen, 1988) for species and for interaction of species \times season, larger samples may well have yielded significance. When the two species were compared for each season by *t*-tests, no species differences were detected in any season (all $P \geq 0.056$). However, the effect sizes (Cohen's *d*) were large (active 2003: MCP, $d = 1.25$, FK, $d = 0.85$; winter 2003–2004: MCP, $d = 0.14$, FK, $d = 0.58$; active 2004: MCP, $d = 0.76$, FK, $d = 0.85$), especially during the active seasons, further suggesting that *C. o helleri* occupied larger home

TABLE 2-1. Summary of number of locations (fixes), home range estimates (100% minimum convex polygon, MCP; 95% fixed kernel, FK; in hectares), mean daily movements (m/d), and Schoener's autocorrelation (t^2/r^2) per each of three seasons for individual male Red Diamond (*Crotalus ruber*, CR) and Southern Pacific (*C. oreganus helleri*, CH) Rattlesnakes.

Species-Snake	Active Season 2003					Winter Season 2003–2004					Active Season 2004				
	Fixes	MCP	FK	m/d	t^2/r^2	Fixes	MCP	FK	m/d	t^2/r^2	Fixes	MCP	FK	m/d	t^2/r^2
CR1	29	4.05	7.53	9.42	1.02	11	0.17	0.20	0.85	2.59	29	3.72	1.62	5.40	0.62
CR2	32	3.80	1.77	5.45	0.67	8	0.01	0.05	1.07	2.76	6	4.50	127.02 ^a	16.46	0.89
CR8	27	1.26	0.73	6.02	1.89	6	0.06	0.03	1.58	1.21	7	0.63	0.52	26.06	2.46
CR12	23	2.36	1.57	6.22	1.46	10	0.10	0.02	2.21	2.67	40	3.58	1.11	9.50	1.52
CR13	23	1.58	0.60	5.76	1.95	9	0.02	0.03	1.04	0.87	39	1.96	1.16	11.96	1.45
CR19	23	0.34	0.15	2.93	1.59	-	-	-	-	-	-	-	-	-	-
CR36	-	-	-	-	-	-	-	-	-	-	13	0.93	0.61	5.39	1.47
Mean	26.2	2.23	2.06	5.97	1.43	8.8	0.07	0.07	1.35	2.02	22.3	2.55	1.00	12.46	1.40
±	±	±	±	±	±	±0.9	±	±	±	±	±	±	±	±	±
1 SE	1.6	0.60	1.12	0.85	0.20		0.03	0.03	0.25	0.40	6.4	0.66	0.20	3.21	0.26
CH1	10	3.22	2.90	12.18	0.86	-	-	-	-	-	-	-	-	-	-
CH2	27	4.82	0.92	13.23	2.07	-	-	-	-	-	-	-	-	-	-
CH3	34	3.46	2.14	14.13	1.32	-	-	-	-	-	-	-	-	-	-
CH5	25	1.98	2.81	4.70	1.16	10	0.01	0.06	0.88	2.80	10	6.10	0.22	25.83	1.94
CH7	23	8.53	15.28	21.79	1.80	10	0.19	0.26	3.69	1.06	37	23.02	9.73	17.39	1.26
CH8	24	6.13	12.38	34.70	1.71	10	0.05	0.05	3.40	1.47	12	4.45	16.39	37.18	2.47
CH33	-	-	-	-	-	-	-	-	-	-	8	0.90	2.60	21.78	1.44
CH39	-	-	-	-	-	-	-	-	-	-	19	3.54	0.17	27.06	0.80
CH42	-	-	-	-	-	-	-	-	-	-	32	3.70	0.84	14.28	1.49
Mean	23.8	4.69	6.07	16.79	1.49	10.0	0.08	0.12	2.66	1.78	19.7	6.95	5.00	23.92	1.57
±	±	±	±	±	±	±	±	±	±	±	±	±	±	±	±
1 SE	3.2	0.96	2.50	4.21	0.18	0.0	0.05	0.07	0.89	0.53	5.0	3.29	2.72	3.31	0.24

^a Regarded as an outlier and excluded from analyses.

ranges than *C. ruber*. Mean home range estimates were two- to five-fold greater for *C. o. helleri* (Table 2-1)

The 100% MCP and 95% FK estimates from individual snakes were positively correlated during the first two seasons (active 2003: $n = 12$, $r^2 = 0.74$, $P < 0.001$; winter 2003–2004: $n = 8$, $r^2 = 0.70$, $P = 0.009$), but not during the third (active 2004: $n = 11$, $r^2 = 0.22$, $P = 0.15$). Although individual MCP estimates were usually larger than corresponding FK estimates during the active season (73.9% of 23 estimates), the FK estimates were more often larger during the inactive season (62.5% of 8 estimates, excluding one tie). In all seasons, the MCP (all $r^2 \leq 0.26$ and $P \geq 0.20$) and FK (all $r^2 \leq 0.27$ and $P \geq 0.19$) estimates were independent of number of fixes.

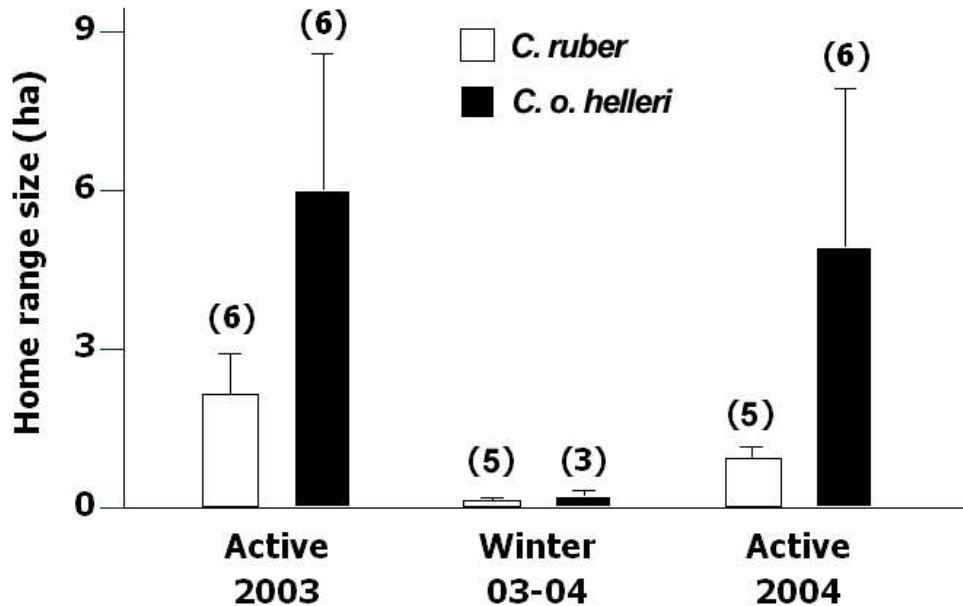


FIG. 2-1. Mean (+ 1 SE) 95% fixed kernel estimates of home range size for adult male Red Diamond Rattlesnakes (*Crotalus ruber*) and Southern Pacific Rattlesnakes (*C. oreganus helleri*) during three seasons at Chino Hills State Park, California. Sample sizes for each mean are within parentheses.

Autocorrelation

Autocorrelation values (Schoener's t^2/r^2 statistic) varied from 0.62 to 2.80 for individual home range estimates, with means for the six cells (2 species \times 3 seasons) ranging from 1.40 to 2.02 (Table 2-1). Schoener values substantially <2.0 are indicative of time dependence between successive relocations (Swihart and Slade, 1985). The ANOVA showed that autocorrelation values were similar for the two species and three seasons, with no interaction (all $P \geq 0.52$; all partial $\eta^2 \leq 0.13$; Table 2-2). Likewise, independent t -tests for each of the three seasons revealed no species differences (all $P \geq 0.65$) and effect sizes were small (all Cohen's $d \leq 0.27$). Autocorrelation values during each of the three seasons were independent of both MCP (all $r^2 \leq 0.02$, $P \geq 0.65$) and FK (all $r^2 \leq 0.14$, $P \geq 0.26$) and number of fixes (all $r^2 \leq 0.10$, $P \geq 0.32$).

Movements

Mean daily movements of individual snakes varied from 2.93–37.18 m/d during the active season to 0.85–3.69 m/d during the winter (Table 2-1). From the ANOVA, the significant main effect of species ($P = 0.037$, partial $\eta^2 = 0.39$) indicated that *C. o. helleri* moved greater distances on average than *C. ruber* (Table 2-2). The differences were most evident during the active seasons, with *C. o. helleri* moving 2.8-fold further in 2003 and 1.9-fold further in 2004 (using species means in Table 2-1). The main effect of season was also significant ($P = 0.001$, partial $\eta^2 = 0.41$), with snakes moving considerably less during the winter compared to the active seasons (*C. ruber* = 14.7% and *C. o. helleri* = 13.1% of their respective active-season movements, calculated from species means in Table 2-1 averaged for the two active seasons). There was no interaction between season and species (Table 2-2). When the two species were compared for each season by t -tests,

mean daily movements differed for each of the two active seasons (active 2003: $t_{10} = 2.52$, $P = 0.031$, Cohen's $d = 1.45$; active 2004: $t_{10} = 2.48$, $P = 0.032$, Cohen's $d = 1.43$), but not for the winter season ($P = 0.12$), though the effect size was substantial (Cohen's $d = 1.13$).

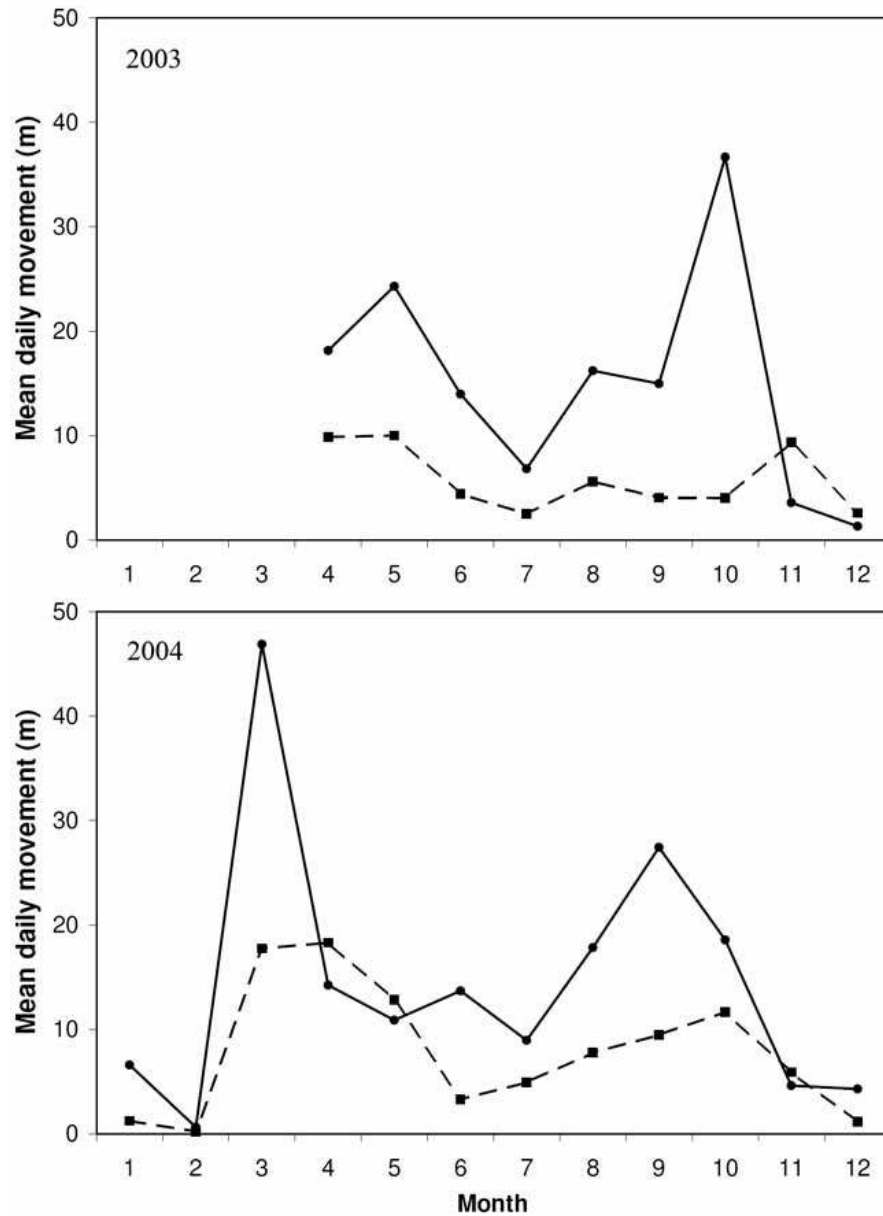


FIG. 2-2. Mean daily movements per month (numbered January–December) of adult male Red Diamond Rattlesnakes (*Crotalus ruber*; dashed lines) and Southern Pacific Rattlesnakes (*C. oreganus helleri*; solid lines) during each of two years. For each mean, $n = 2-6$.

Movements were positively correlated with MCP in one season (active 2003: $r^2 = 0.62$, $P = 0.002$), but not in the others (both $r^2 \leq 0.18$ and $P \geq 0.30$). Movements were similarly associated with FK in one season (active 2003: $r^2 = 0.64$, $P = 0.002$), but not in the others (both $r^2 \leq 0.26$ and $P \geq 0.11$). Movements were independent of number of fixes in all seasons (all $r^2 \leq 0.26$ and $P \geq 0.09$), but were weakly positively associated with autocorrelation in one season (active 2004: $r^2 = 0.33$, $P = 0.049$; other seasons: $r^2 \leq 0.21$ and $P \geq 0.25$). Although not amenable to statistical analysis, monthly patterns of activity (Fig. 2-2) revealed peaks in both spring and late summer/fall, with relatively less activity occurring during the summer months.

Individuals of both species moved on occasion during the winter, demonstrating a lack of overwintering single-site fidelity. Neither species used communal hibernacula.

TABLE 2-2. Summary of analysis of variance (ANOVA) results for home range estimates (100% minimum convex polygon, MCP; 95% fixed kernel, FK), mean daily movements, and autocorrelation (t^2/r^2) for two species of rattlesnake over three seasons (see Table 2-1). Results include degrees of freedom (df), F -value, probability (P), and effect size (adjusted partial η^2).

Dependent Variable	Season				Species				Interaction			
	df	F	P	η^2	df	F	P	η^2	df	F	P	η^2
MCP	2,8	8.89	0.041	0.47	1,4	2.08	0.223	0.29	2,8	1.66	0.250	0.25
FK	2,8	5.39	0.033	0.43	1,4	2.96	0.160	0.32	2,8	1.97	0.201	0.25
Movements	2,12	15.35	0.001	0.41	1,6	7.14	0.037	0.39	2,12	2.18	0.156	0.20
t^2/r^2	2,8	0.51	0.621	0.11	1,4	0.49	0.524	0.11	2,8	0.62	0.562	0.13

Mating Phenology

At our study site, we observed distinctly different use of mating seasons in the two species (Table 2-3). *Crotalus ruber* exhibited accompaniment, courtship, and copulation only during spring (2 February–7 April), whereas *C. o. helleri* exhibited sexual behaviors during both spring (16 February–24 April) and late summer/fall (11 September–3 October). For total observations (accompaniment and copulations), the asymmetry between species and season was significant (Cramer’s $V = 0.41$, $P = 0.013$). When additional data from existing literature were added to our observations (Table 2-3), the asymmetry was even stronger (Cramer’s $V = 0.53$, $P < 0.001$).

TABLE 2-3. Number of sexual interactions observed in Red Diamond (*Crotalus ruber*) and Southern Pacific (*C. oreganus helleri*) Rattlesnakes, including male-female pairs interacting (accompaniment, sometimes including courtship) or copulating at our study site during spring and late summer/fall. Numbers in parentheses represent sum of our observations and reports from existing literature.^a

Sexual Interactions	Spring		Late Summer/Fall	
	<i>C. ruber</i>	<i>C. o. helleri</i>	<i>C. ruber</i>	<i>C. o. helleri</i>
Accompaniment	10 (19)	8 (8)	0 (0)	3 (3)
Copulation	9 (27)	5 (6)	0 (0)	2 (5)
Totals	19 (46)	13 (14)	0 (0)	5 (8)

^a Sources: Linsdale (1932), Armstrong and Murphy (1979), Klauber (1972), Grismer (2002), Brown et al. (this volume).

Discussion

We expected to see seasonal differences in home range size and movements, with both species occupying larger home ranges and moving greater distances during the active season than during the winter. However, we had no *a priori* expectations of finding the species differences that were detected. In the sections that follow, we emphasize these species differences, but also render comparisons to other studies when relevant.

Home Range Size

Although we did not detect a statistical difference in home range size between the two species, effect sizes were large enough to suggest that a disparity exists, with *C. o. helleri* occupying two- to five-fold larger home ranges than *C. ruber* at our study site. Unfortunately, the relatively small sample size resulting from high levels of predation on *C. o. helleri* (see Methods) reduced the power of our statistical analyses, but practical significance (effect size) is often more meaningful, as it can be interpreted apart from sample size effects (Cohen, 1988). During winter, the two species likely occupy similarly-sized home ranges, and these are much smaller than those used during the active season. Although we did not track females during this study, *C. ruber* females use significantly smaller home ranges than males (Brown et al., this volume; Greenberg, 2002;). We attribute species differences in home range size to the different preferred habitats, as discussed in the next section.

A comparison of 100% MCP estimates from three locations in southern California suggests that coastal populations of *C. ruber* occupy smaller home ranges than those of desert populations. At our coastal site, the seven adult males averaged 2.4 ha, with

individuals occupying 0.3–4.5 ha (based on 6–40 fixes during the 9-month active season over 2 yr; Table 2-1). Five telemetered adult males at a coastal San Diego County location averaged 2.8 ha, with individuals ranging from 1.1–4.4 ha (based on 18–79 unique fixes during up to a 4-yr duration; Brown et al., this volume). In contrast to coastal populations, five telemetered adult males at a desert location in Riverside County averaged 25.8 ha, with individuals ranging from 7.2–52.5 ha (based on an unknown number of fixes over 381–1,000 d; Greenberg, 2002). Intraspecific variation in home range size could be attributed to differential availability and distribution of resources in coastal and desert environments (Gregory et al., 1987). One might expect that reliance on communal hibernacula would increase home range size, with snakes often dispersing great distances during the active season to reduce interspecific competition (Brown, 1993; Jørgensen et al., this volume; Martin, 1992; Reinert and Zappalorti, 1988; see further comments below). However, whereas snakes at our site and at the desert Riverside County location (Greenberg, 2002) did not use communal overwintering sites, those at the coastal San Diego County site did so, and their home ranges were relatively small (Brown et al., this volume). Unfortunately, we cannot compare our results from *C. o. helleri* to other locations due to the absence of such studies.

In our study, MCP and FK estimates showed close correspondence (with CR2 being the one exception in Table 2-1). Although both home range estimators are sample size-dependent (MCP increasing and FK decreasing with increasing sample size; Seaman et al., 1999) and FK estimates are especially sensitive to autocorrelation (Powell, 2000), we found no overt influence of number of fixes or autocorrelation on our estimates. The consequences of autocorrelation are frequently ignored in studies of home range size,

though the sedentary nature of snakes, and reptiles in general, can often result in autocorrelation (Figueroa et al., this volume; Row and Blouin-Demers, 2006).

Movements and Mating Phenology

Crotalus ruber not only used a smaller home range size than *C. o. helleri*, but also moved significantly less. We hypothesize two aspects of the biology of each species that likely contributed to the differences observed in active-season movements: habitat use and the timing and frequency of mating seasons.

The availability and distribution of preferred habitat have been shown to affect both annual (Reinert, 1993) and seasonal (Marshall et al., 2006) movements of rattlesnakes. At our site, *C. ruber* and *C. o. helleri* exhibited significant differences in habitat use (Dugan and Hayes, 2005, unpubl. data). Preferred habitat of *C. ruber* at our site—cactus primarily, and chaparral—is sparsely distributed and restricted to a series of south-facing hillsides. Movements of *C. ruber* throughout the study period were primarily confined to moves between and within clusters of *Opuntia* cactus patches. Several individuals spent virtually an entire active season within a single cactus patch. In contrast, preferred habitat of *C. o. helleri*—grassland and riparian—is widely and more continuously distributed throughout the site. The greater mean distances moved annually by *C. o. helleri* may be associated with the less-restricted abundance of grassland and riparian habitats.

Reproductive condition also dramatically affects the movements of both male and female rattlesnakes. During mating season, male rattlesnakes search extensively for females to mate (e.g., Aldridge and Brown, 1995; Ashton, 2003; Brown et al., this volume; Cardwell, 2008; Duvall et al., 1992; Goode et al., this volume; Jellen et al.,

2007; Marshall et al., 2006; Prival et al., 2002; Sealy, 2002; Secor, 1992; Waldron et al., 2006a). Female rattlesnakes, in contrast, do not actively search for mates (Duvall and Schuett, 1997), and typically exhibit smaller home ranges and reduced movements, with gravid individuals being most sedentary. At our study site, male *C. o. helleri* moved significantly greater distances than male *C. ruber*. The difference may result, in part, from the different mating phenology of the two species. *Crotalus ruber* at our site appears to mate exclusively in the spring (Table 2-3). A comprehensive review of the literature suggests that this is a range-wide phenomenon (Aldridge and Duvall, 2002; Brown et al., this volume; Campbell and Lamar, 2004; Goldberg, 1999; Greenberg, 2002; Grismer, 2002; Klauber, 1972), as we were unable to locate any published records of reproductive activity in *C. ruber* outside of the well-documented spring mating period. *Crotalus o. helleri*, in contrast, mates during both spring and late summer/fall at our site (Table 2-3), and probably does so throughout its range (Aldridge, 2002). Males of both species at our study site exhibited increased movements during the spring mating season, but late summer/fall movements by *C. o. helleri* appeared to be greater than those of *C. ruber* (Fig. 2-2). Thus, the finding that *C. o. helleri* moves significantly greater distances than *C. ruber* during the active season may reflect the additional late summer/fall mating season of *C. o. helleri*.

The reason for the marked difference between *C. ruber* and *C. o. helleri* in the timing and frequency of mating seasons remains unclear. A similar disparity exists for sympatric *C. atrox* (late summer/fall and spring mating) and *C. molossus* (spring mating) in Arizona, with *C. atrox* exhibiting two corresponding peaks in testosterone and *C. molossus* only one (Schuett et al., 2005). Thus, the differences may be physiologically

based if the behaviors are hormonally dependent, but clearly do not derive from ambient environmental factors (e.g., photoperiod, temperature, precipitation) and more likely relate to evolutionary history (Aldridge and Duvall, 2002; Schuett et al., 2002, 2005). However, because reproductive isolation between sympatric rattlesnakes almost certainly results from pheromone differentiation (Shine et al., 2002, 2004), and the costs borne by males to locate females by following pheromone trails can be high (Aldridge and Brown, 1995; Aldridge and Duvall, 2002; McGowan and Madison, this volume), temporal segregation of mating seasons may have originated from competitive mechanisms if the costs for discriminating conspecific from heterospecific female pheromone trails are high. Such costs might be expected to be higher during the late summer/fall mating season, as both *C. ruber* and *C. o. helleri* at our study site often overwinter in relatively close proximity on south-facing slopes, where mate location would be facilitated in spring (Dugan and Hayes, unpubl. data).

The annual movements of rattlesnakes vary substantially across species and may relate to intraspecific competition. Some populations are clearly migratory, typically moving substantial distances between their communal hibernaculas and their active-season home ranges (e.g., Brown, 1993; Duvall and Schuett, 1997; Jørgensen et al., this volume; Macartney et al., 1988). Migratory populations generally inhabit regions that experience extreme winter temperatures with limited suitable overwintering sites (for an exception, see Harvey and Weatherhead, 2006). However, rattlesnake populations in milder climates, such as those at our study site, frequently hibernate solitarily without strong site fidelity and lack annual unidirectional movements (e.g., Greenberg, 2002; Secor, 1992). Home range size may also be smaller in non-migratory populations. We

concur with Greenberg (2002) that differences in movements and spatial use by individuals in these populations likely arise from differences in competition. Snakes at communal hibernacula face higher levels of intraspecific (and often interspecific) competition and, therefore, must disperse to a greater extent than snakes that hibernate solitarily.

Niche Partitioning

Niche separation between closely-related sympatric species can be achieved via differences in food (type or size) or in use of spatial (macrohabitat or microhabitat), temporal (diel or seasonal activity patterns), or thermal resources (Saint Girons, 1978; Schoener, 1974). Our findings suggest that sympatric populations of *C. ruber* and *C. o. helleri*, like other sympatric rattlesnakes (Beck, 1995; Mendelson and Jennings, 1992; Pough, 1966; Reynolds and Scott, 1982; Steen et al., 2007; Waldron et al., 2006b) and vipers (Luiselli, 2006a,b; Luiselli et al., 2007; Reinert, 1984) studied to date, primarily partition the habitat to reduce interspecific competition. However, unlike other sympatric rattlesnakes investigated thus far, *C. ruber* and *C. o. helleri* also differ in their use of spatial and temporal resources, though probably not as a direct result of competitive mechanisms. Although diet may vary among sympatric rattlesnakes (e.g., Clark, 2002; Holycross et al., 2002), including between *C. ruber* and *C. o. helleri* at our study site (Dugan, unpubl. data), rattlesnakes are often opportunistic feeders (within broader categories of preferred prey types, such as lizards and mammals; e.g., Avila-Villegas et al., 2007; Campbell and Lamar, 2004; Clark, 2002; Holycross et al., 2002; Klauber, 1972), and dietary differences may relate primarily to prey availability in the different preferred habitats and, secondarily, to size differences (gape-limited constraints) between

adults (Reynolds and Scott, 1982). We imagine that diet might be partitioned more so than habitat among some sympatric rattlesnakes that differ substantially in adult size and coexist in environments with limited habitat variability (e.g., *C. atrox* and *C. cerastes* in creosote [*Larrea tridentata*] desert flats). Apart from differences in mating seasons, we found no evidence that *C. ruber* and *C. o. helleri* further partition temporal resources. In terms of diel activity, we found both species active primarily during morning and evening hours, with some shift to nocturnal activity during hot weather (Dugan, unpubl. data). In terms of seasonal activity, we found *C. ruber* to be relatively sedentary compared to *C. o. helleri*, but the timing and duration of the active season were similar. Although we have not yet examined body temperature data, we are doubtful that thermal resources are partitioned between these two species. Perhaps further study of other sympatric rattlesnakes will reveal examples wherein food, temporal, or thermal resources are substantially partitioned to facilitate coexistence.

Acknowledgments

All research was carried out under permits issued to the senior author by the California Department of Fish and Game and by Chino Hills State Park (CHSP). We thank ranger Bart Grant of CHSP for his assistance in our research. We received significant technical and field support from numerous individuals, including Mike Cardwell, Brian McGurty, Chris Rodriguez, Sean Bush, and Kent Beaman. The Loma Linda University Department of Earth and Biological Sciences provided financial support for the studies. This project was approved by the Loma Linda University Institutional Animal Care and Use Committee and was conducted under a permit issued by the California Department of Fish and Game.

References

- ALDRIDGE, R. D. 2002. The link between mating season and male reproductive anatomy in the rattlesnakes *Crotalus viridis oreganus* and *Crotalus viridis helleri*. *Journal of Herpetology* 36:295–300.
- ALDRIDGE, R. D., AND W. S. BROWN. 1995. Male reproductive cycle, age at maturity, and cost of reproduction in the timber rattlesnake (*Crotalus horridus*). *Journal of Herpetology* 29:399–407.
- ALDRIDGE, R. D., AND D. DUVALL. 2002. The evolution of the mating season in the pitvipers of North America. *Herpetological Monographs* 16:1–25.
- ARMSTRONG, B. L., AND J. B. MURPHY. 1979. The natural history of Mexican rattlesnakes. University of Kansas Publications, Museum of Natural History 51:1–88.
- ASHTON, K. G. 2003. Movements and mating behaviour of adult male midget faded rattlesnakes, *Crotalus oreganus concolor*, in Wyoming. *Copeia* 2003:190–194.
- ASHTON, K. G., AND A. DE QUEIROZ. 2001. Molecular systematics of the western rattlesnake, *Crotalus viridis* (Viperidae), with comments on the utility of the D-loop in phylogenetic studies of snakes. *Molecular Phylogenetics and Evolution* 21:176–189.
- AVILA-VILLEGAS, H., M. MARTINS, AND G. ARNAUD. 2007. Feeding ecology of the endemic rattleless rattlesnake, *Crotalus catalinensis*, of Santa Catalina Island, Gulf of California, Mexico. *Copeia* 2007:80–84.
- BEAMAN, K. R., AND E. A. DUGAN. 2006. *Crotalus ruber* (red diamond rattlesnake). *Catalogue of American Amphibians and Reptiles* 840:1–17.
- BECK, D. 1995. Ecology and energetics of three sympatric rattlesnake species in the Sonoran Desert. *Journal of Herpetology*. 29:211–223.
- BROWN, W. S. 1993. Biology, status, and management of timber rattlesnakes (*Crotalus horridus*): a guide for conservation. SSAR Herpetological Circular No. 22.
- CAMPBELL, J. A., AND W. W. LAMAR. 2004. *The Venomous Reptiles of the Western Hemisphere*. Cornell University Press, Ithaca, New York.
- CARDWELL, M. D. 2008. The reproductive ecology of Mohave rattlesnakes. *Journal of Zoology* 274:65–76.
- CLARK, R. 2002. Diet of the timber rattlesnake, *Crotalus horridus*. *Journal of Herpetology* 36:494–499.

- COHEN, J. 1988. *Statistical Power Analysis for the Behavioral Sciences* (2nd ed.). Erlbaum, Hillsdale, New Jersey.
- CONOVER, W. J. 1999. *Practical Nonparametric Statistics*, 3rd ed. John Wiley and Sons, Inc., New York, New York.
- DILLER, L. V., AND R. L. WALLACE. 2002. Growth, reproduction, and survival in a population of *Crotalus viridis oregonus* in north central Idaho. *Herpetological Monographs* 16:26–45.
- DUGAN, E. A., AND W. K. HAYES. 2005. Comparative ecology of red diamond (*Crotalus ruber*) and southern Pacific (*Crotalus helleri*) rattlesnakes in southern California. Pg. 27 in *Program and Abstracts of the Biology of the Rattlesnakes Symposium*. Loma Linda University, Loma Linda, California.
- DUVALL, D., AND G. W. SCHUETT. 1997. Straight-line movements and competitive mate searching in prairie rattlesnakes, *Crotalus viridis viridis*. *Animal Behavior* 54:329–334.
- DUVALL, D., S. J. ARNOLD, AND G. W. SCHUETT. 1992. Pitviper mating systems: ecological potential, sexual selection, and microevolution. Pp. 169–184 in J. A. Campbell and E. D. Brodie Jr. (eds.). *Biology of the Pitvipers*. Selva Press, Tyler, Texas.
- GOLDBERG, S. R. 1999. Reproduction in the red diamond rattlesnake in California. *California Fish and Game* 85:177–180.
- GOODMAN, R. H. 1997. The biology of the southwestern pond turtle (*Clemmys marmorata pallida*) in the Chino Hills State Park and the west fork of the San Gabriel River. M.S. Thesis, California State University, Fullerton.
- GREENBERG, D. B. 2002. The ecology of movement and site selection in desert rattlesnakes (*Crotalus mitchellii* and *Crotalus ruber*) of the southwestern United States. Ph.D. Dissertation, University of California, Santa Barbara.
- GREGORY, P. T., J. M. MACARTNEY, AND K. W. LARSEN. 1987. Spatial patterns and movements. Pp. 366–395 in R. A. Seigel, J. T. Collins, and S. S. Novak (eds.), *Snakes: Ecology and Evolutionary Biology*. McGraw-Hill, Inc., New York, New York.
- GRISMER, L. L. 2002. *Amphibians and Reptiles of Baja California Including its Pacific Islands and the Islands in the Sea of Cortes*. University of California Press, Berkeley, California.
- HARDY, D. L., AND H. W. GREENE. 1999. Surgery on rattlesnakes in the field for implantation of transmitters. *Sonoran Herpetologist* 12:25–27.

- HARVEY, D. S., AND P. J. WEATHERHEAD. 2006. Hibernation site selection by eastern massasauga rattlesnakes (*Sistrurus catenatus catenatus*) near their northern range limit. *Journal of Herpetology* 40:66–73.
- HOLYCROSS, A. T., C. W. PAINTER, D. B. PRIVAL, D. E. SWANN, M. J. SCHROFF, T. EDWARDS, AND C. R. SCHWALBE. 2002. Diet of *Crotalus lepidus klauberi* (banded rock rattlesnake). *Journal of Herpetology* 36:589–597.
- HOVEY, F. W. 1999. The Home Ranger. British Columbia Forest Service Research Branch, Revelstoke, British Columbia, Canada.
- JELLEN, B. C., D. B. SHEPARD, M. J. DRESLIK, AND C. A. PHILLIPS. 2007. Male movement and body size affect mate acquisition in the eastern massasauga (*Sistrurus catenatus*). *Journal of Herpetology* 41:451–457.
- JENNINGS, M. R., AND M. P. HAYES. 1994. Amphibian and Reptile Species of Special Concern in California. California Department of Fish and Game, Rancho Cordova, California.
- KELLER, T. K. 1992. Relationship of plant ecology and hydrology in Aliso Canyon riparian zone, Chino Hills, southern California. M.S. Thesis, California State University, Fullerton.
- KIE, J. G., J. A. BALDWIN, AND C. J. EVANS. 1994. Calhome: Home Range Analysis Program. U.S. Forest Service Pacific Southwest Research Station, Fresno, California.
- KLAUBER, L. M. 1972. Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind, 2nd ed. University of California Press, Berkeley, California.
- LAVER, P. N., AND M. J. KELLY. 2008. A critical review of home range studies. *Journal of Wildlife Management*. 72:290–298.
- LINSDALE, J. M. 1932. Amphibians and reptiles from Lower California. *University of California Publications in Zoology* 38:345–386.
- LUISELLI, L. 2006a. Resource partitioning and interspecific competition in snakes: the search for general geographical and guild patterns. *Oikos* 114:193–211.
- LUISELLI, L. 2006b. Site occupancy and density of sympatric gaboon Viper (*Bitis gabonica*) and nose-horned viper (*Bitis nasicornis*). *Journal of Tropical Ecology* 22:555–564.
- LUISELLI, L., E. FILIPPI, AND E. DI LENA. 2007. Ecological relationships between sympatric *Vipera aspis* and *Vipera ursinii* in high- altitude habitats of central Italy. *Journal of Herpetology*. 41:378–384.

- MACARTNEY, J. M., P. T. GREGORY, AND K. W. LARSEN. 1988. A tabular survey of data on movements and home ranges of snakes. *Journal of Herpetology* 22:61–73.
- MARSHALL, J. C., JR., J. V. MANNING, AND B. A. KINGSBURY. 2006. Movement and macrohabitat selection of the eastern massasauga in a fen habitat. *Herpetologica* 62:141–150.
- MARTIN, W. H. 1992. Phenology of the timber rattlesnake (*Crotalus horridus*) in an unglaciated section of the Appalachian Mountains. Pp. 169–184 in J. A. Campbell and E. D. Brodie, Jr. (eds.), *Biology of the Pitvipers*. Selva, Tyler, Texas.
- MENDELSON, J. R., III, AND W. B. JENNINGS. 1992. Shifts in the Relative Abundance of Snakes in a Desert Grassland. *Journal of Herpetology* 26:38–45.
- MERTLER, C. A., AND R. A. VANNATTA. 2004. *Advanced and Multivariate Statistical Methods: Practical Application and Interpretation* (3rd ed). Pyrczak Publishing, Los Angeles, California.
- PIANKA, E. 1981. Competition and niche theory. Pp. 167–196 in R. May (ed.), *Theoretical Ecology. Principles and Applications*. Blackwell, Oxford, United Kingdom.
- POUGH, F. H. 1966. Ecological relationships of rattlesnakes in southeastern Arizona with notes on other species. *Copeia* 1966:676–683.
- POWELL, R. A. 2000. Animal home ranges and territories and home range estimators. Pp. 65–110 in L. Boitani and T. K. Fuller (eds.), *Research Techniques in Animal Ecology*. Columbia University Press, New York, New York.
- PRIVAL, D. B., M. J. GOODE, D. E. SWANN, C. R. SCHWALBE, AND M. J. SCHROFF. 2002. Natural history of a northern population of twin-spotted rattlesnakes, *Crotalus pricei*. *Journal of Herpetology* 36:598–607.
- REINERT, H. K. 1984. Habitat separation between sympatric snake populations. *Ecology* 65:478–486.
- REINERT, H. K. 1993. Habitat selection in snakes. Pp. 201–240 in R. A. Seigel and J. T. Collins (eds.), *Snakes: Ecology and Behavior*. McGraw-Hill, Inc., New York, New York.
- REINERT, H. K., AND D. CUNDALL. 1982. An improved surgical implantation method for radio-tracking snakes. *Copeia* 1982:702–705.
- REINERT, H. K., AND R. T. ZAPPALORTI. 1988. Timber rattlesnakes (*Crotalus horridus*) of the Pine Barrens: their movement patterns and habitat preference. *Copeia* 1988:964–978.

- REYNOLDS, R. P., AND N. J. SCOTT, JR. 1982. Use of a mammalian resource by a Chihuahuan snake community. Pp. 99–118 in N. J. Scott, Jr. (ed.), *Herpetological Communities*. U.S. Dept. Interior, Fish and Wildlife Service, Wildlife Research Report 13.
- ROW, J. R., AND G. BLOUIN-DEMERS. 2006. Kernels are not accurate estimators of home-range size for herpetofauna. *Copeia* 2006:797–802.
- SAINT GIRONS, H. 1978. Thermorégulation comparé de vipères d'Europe. Etude biotéléométrique. *Revue d'Ecologie (La Terre et la Vie)* 32:417–439.
- SAMPSON, G. T. 1985. A flora of Chino Hills State Park. M.A. Thesis, California State University, Fullerton.
- SCHOENER, T. W. 1974. Resource partitioning in ecological communities. *Science* 185:27–39.
- SCHUETT, G. W., S. L. CARLISLE, A. T. HOLYCROSS, J. K. O'LEILE, D. L. HARDY, SR., E. A. VAN KIRK, AND W. J. MURDOCH. 2002. Mating system of male Mojave rattlesnakes (*Crotalus scutulatus*): seasonal timing of mating, agonistic behavior, spermatogenesis, sexual segment of the kidney, and plasma sex steroids. Pp. 515–532 in G. W. Schuett, M. Höggren, M. E. Douglas, and H. W. Greene, *Biology of the Vipers*. Eagle Mountain Publishing, Eagle Mountain, Utah.
- SCHUETT, G. A., D. L. HARDY, SR., H. W. GREENE, R. L. EARLEY, M. S. GROBER, E. A. VAN KIRK, AND W. J. MURDOCH. 2005. Sympatric rattlesnakes with contrasting mating systems show differences in seasonal patterns of plasma sex steroids. *Animal Behavior* 70:257–266.
- SEALY, J. B. 2002. Ecology and behavior of the timber rattlesnake (*Crotalus horridus*) in the Upper Piedmont of North Carolina: identified threats and conservation recommendations. Pp. 561–578 in G. W. Schuett, M. Höggren, M. E. Douglas, and H. W. Greene, *Biology of the Vipers*. Eagle Mountain Publishing, Eagle Mountain, Utah.
- SEAMAN, D. E., J. J. MILLSPAUGH, B. J. KERNOHAN, G. C. BRUNDIGE, K. J. RAEDEKE, AND R. A. GITZEN. 1999. Effects of sample size on kernel home range estimators. *Journal of Wildlife Management*. 63:739–747.
- SECOR, S. M. 1992. A preliminary analysis of the movement and home range size of the Sidewinder, *Crotalus cerastes*. Pp. 169–184 in J. A. Campbell and E. D. Brodie, Jr. (eds.), *Biology of the Pitvipers*. Selva, Tyler, Texas.
- SEIGEL, R. A., AND M. A. PILGRIM. 2002. Long-term changes in movement patterns of Massasaugas (*Sistrurus catenatus*). Pp. 405–512 in G. W. Schuett, M. Höggren,

- M. E. Douglas, and H. W. Greene (eds.), *Biology of the Vipers*. Eagle Mountain Publishing, Eagle Mountain, Utah.
- SHINE, R., B. PHILLIPS, H. WAYE, M. LEMASTER, AND R. T. MASON. 2004. Species-isolating mechanisms in a mating system with male mate choice (garter snakes, *Thamnophis* spp.). *Canadian Journal of Zoology* 82:1091–1098.
- SHINE, R., R. N. REED, S. SHETTY, M. LEMASTER, AND R. T. MASON. 2002. Reproductive isolating mechanisms between two sympatric sibling species of sea-snakes. *Evolution* 56:1655–1662.
- SPSS. 2003. SPSS for Windows, version 12.0. SPSS, Inc., Chicago, Illinois.
- STEBBINS, R.C. 2003. *Western Reptiles and Amphibians*, 3rd ed. Houghton Mifflin, Boston, Massachusetts.
- STEEN, D. A., L. L. SMITH, L. M. CONNER, J. C. BROCK, AND S. K. HOSS. 2007. Habitat use of sympatric rattlesnake species within the Gulf Coastal Plain. *Journal of Wildlife Management*. 71:759–764.
- SWIHART, R. K., AND N. A. SLADE. 1985. Influence of sampling interval on estimates of home-range size. *Journal of Wildlife Management*. 49:1019–1025.
- TOFT, C. A. 1985. Resource partitioning in amphibians and reptiles. *Copeia* 1985:1–21.
- VITT, L. J. 1987. Communities. Pp. 335–365 in R. A. Seigel, J. T. Collins, and S. S. Novak (eds.), *Snakes: Ecology and Evolutionary Biology*. MacMillan Publ. Co., New York, New York.
- WALDRON, J. L., J. D. LANHAM, AND S. H. BENNETT. 2006a. Using behaviorally-based seasons to investigate canebrake rattlesnake (*Crotalus horridus*) movement patterns and habitat selection. *Herpetologica* 62:389–398.
- WALDRON, J. L., S. H. BENNETT, S. M. WELCH, M. E. DORCAS, J. D. LANHAM, AND W. KALINOWSKY. 2006b. Habitat specificity and home-range size as attributes of species vulnerability to extinction: a case study using sympatric rattlesnakes. *Animal Conservation* 9:414–420.
- WALTER, G. H. (1991). What is resource partitioning? *Journal of Theoretical Biology* 150:137–143.

CHAPTER THREE
NICHE SEPARATION AND RESOURCE PARTITIONING IN THE
SYMPATRIC RATTLESNAKES *CROTALUS RUBER* AND *C.*
OREGANUS HELLERI IN SOUTHERN CALIFORNIA

ERIC A. DUGAN^{1,2} AND WILLIAM K. HAYES¹

¹*Department of Earth and Biological Sciences, Loma Linda University,
Loma Linda, CA 92350 USA*

Abstract

As a major selective force of ecological divergence and speciation, interspecific competition often influences the behavior and ecology of sympatric organisms, and can lead to partitioning of resources. Sympatric snake species appear to partition primarily trophic resources; however, sympatric viper species, similar to most other vertebrates, tend to partition habitats rather than food resources. We examined resource use by two sympatric species, the Red Diamond (*Crotalus ruber*) and Southern Pacific (*C. oregonus helleri*) Rattlesnakes, in Chino Hills State Park, California. Using radio-telemetry and mark-recapture from March 2003 through March 2010, we obtained data from 83 *C. ruber* and 110 *C. o. helleri* on all four major niche axes, including space use (macrohabitat and microhabitat), thermal attributes of microhabitat use, temporal aspects of resource use (seasonal and circadian activity), and diet (prey species and size). Compositional and logistic regression analyses revealed differential and non-random use of macrohabitats (vegetation communities) by the two species. Additional multivariate and contingency analyses revealed similar use of microhabitat (below/above ground, arboreal), seasonal, and circadian resources (seasonal and daily patterns were similar, though *C. o. helleri* engaged in higher levels of locomotion and sexual activity), but differential use of thermal (*C. ruber* warmer) and dietary (both prey species and size) resources. Pianka's and Czekanowski's indices revealed low niche overlap for prey species, moderate overlap of macrohabitat, and broad overlap of microhabitat, thermal and temporal (seasonal and circadian) resources, and prey size. However, Monte Carlo simulations suggested that only two niche features differed significantly from random: thermal resources (greater overlap than expected, presumably due to physiological

constraints) and prey size (less overlap than expected, possibly due to body size differences between snake species and differential prey availability in preferred macrohabitats). We conclude that niche partitioning is minimal or absent between these species, and needs closer examination among other sympatric viper species.

Introduction

As a major selective force of ecological divergence and speciation (Schluter, 2000; Ackermann and Doebeli, 2004; Pearman et al., 2007), interspecific competition often influences the behavior and ecology of sympatric organisms (Goodyear and Pianka, 2008; Schettino et al., 2010). Although often difficult to measure (Reichenbach and Dalrymple, 1980; Toft, 1985), competition among species occupying similar niche guilds can become intense as organisms compete for access to limited resources such as food and space (e.g., Schoener, 1974; Gerstell and Bednarz, 1999; Kozłowski et al., 2008).

Niche partitioning resulting from differential resource use allows ecologically similar species to coexist (Gause, 1934; Schoener, 1974; Luiselli, 2006a; Pfennig et al., 2006; Desbiez et al., 2009). Niche theory predicts that, in cases of interspecific competitive coexistence, either one or both species will alter their niche to a degree that allows cohabitation of a given environ, thereby reducing the intensity of competition (Gause, 1934; Pianka, 1981; Walter, 1991; Arjo et al., 2002; Cadotte, 2007; Luiselli et al., 2007; Pearman et al., 2007). In cases where niche differentiation is precluded by biological settings, competition can result in decreased fitness (i.e., growth, fecundity, or survivorship) of the weaker species (Reichenbach and Dalrymple, 1980; Townsend et al., 2008). Niche separation can be achieved along four major niche axes: spatial separation

(via microhabitat or macrohabitat use), temporal avoidance (diel or seasonal), dietary differences (type or size), or use of thermal resources (Schoener, 1974; Saint Girons, 1978; Luiselli, 2006a).

Considered excellent models for ecological studies (Shine and Bonnet, 2000), snakes are ideally suited for studies of interspecific competition (Luiselli, 2006a). In recent decades, studies of snake communities have revealed various aspects of snake biology that are apparently affected by the presence of competitors, including diet (e.g., Luiselli, 2003; Luiselli and Akani, 2003; Hartmann and Marques, 2005; Edgehouse, 2008; Halstead et al., 2008) and habitat use (e.g., Beck, 1995; Laurent and Kingsbury, 2003; Luiselli et al., 2007). In his review of resource partitioning among amphibians and reptiles, Toft (1985) suggested that sympatric snakes primarily partition food resources, a form of niche partitioning atypical among vertebrates. A more recent review by Luiselli (2006a) supported Toft's findings for several families and habitat scenarios, but contrasted with Toft in showing that sympatric viperids usually partition space. This conclusion suggests that food may not be a limited resource among most vipers, and thus not a source of exploitive interspecific competition (Reichenbach and Dalrymple, 1980).

Studies of resource partitioning among North American viperids, although limited, have been interpreted as support for Luiselli's (2006a) conclusion of habitat partitioning. Differential habitat use was documented among sympatric populations of the rattlesnakes *Crotalus atrox*, *C. molossus*, and *C. scutulatus* in the Sonoran Desert of southeast Arizona and southwestern New Mexico (USA) and Chihuahua (Mexico; Pough, 1966; Reynolds and Scott, 1982; Mendelson and Jennings, 1992). Similarly, Beck (1995) showed use of different habitats by sympatric *C. atrox*, *C. molossus*, and *C. tigris*

in Arizona. Sympatric eastern species also appear to partition habitat, including the rattlesnakes *C. horridus* and *C. adamanteus* (Waldron et al., 2006; Steen et al., 2007), and *C. horridus* and the copperhead *Agkistrodon contortrix* (Reinert, 1984). To date, no evidence for niche separation among other axes (temporal, diet, or thermal resources) has been found among North American viperids. However, two sympatric species of European *Vipera* partition dietary resources (Luiselli et al., 2007), as do two sympatric species of African *Bitis* (Luiselli and Akani, 2003; Luiselli, 2006b).

A major shortcoming of prior studies, particularly from North America, is that conclusions regarding possible niche partitioning were based solely on statistical differences in resource use between two or more species, and usually on a single resource axis. Differences in resource use could arise from a variety of sources, including competitive interactions, phylogenetic divergence, physiological constraints, and random processes. Finding species differences in resource use is not sufficient to demonstrate niche partitioning (Connell, 1980). Niche indices (MacArthur and Levins, 1967; Pianka, 1973; Feinsinger et al., 1981) and null models (Gotelli and Graves, 1996) have been developed to better understand the causes of differential resource use. The null models generate “pseudo-communities” based on resource use data from real life closely-related sympatric species and test whether the amount of niche overlap differs significantly from random.

In southwestern North America, multiple rattlesnake species frequently overlap widely (Klauber, 1972; Stebbins, 1985; Grismer, 2002; Campbell and Lamar, 2004). As one example, the red diamond (*Crotalus ruber*) and southern Pacific (*C. oreganus helleri*) rattlesnakes occupy sympatric ranges throughout large portions of southern

California (USA) and Baja California Norte (Mexico; Grismer, 2002; Beaman and Dugan, 2006). The close phylogenetic relationship (Murphy et al., 2002) and extensive overlap of ranges, habitat, and general life histories (seasonal activity and feeding ecologies) render these two species ideal candidates for exploring potential niche separation and interspecific competition (Dugan et al., 2008).

In this study, we examined resource use for each of the major niche axes of sympatric *C. ruber* and *C. o. helleri* in a coastal canyon of southern California. Our purposes were to compare differential use of 1) space (macrohabitat and microhabitat), 2) thermal resources, 3) temporal resources (seasonal and circadian activity), and 4) diet by the two species. We also examined 5) whether patterns of niche overlap in resource use could be attributed to niche partitioning or non-competitive processes.

Material and Methods

Study Species

The red diamond rattlesnake (*C. ruber*) ranges from San Bernardino County, California, USA, south to the tip of the Baja Peninsula, Baja California Sur, Mexico. Insular populations exist on the Gulf of California islands of Angel de la Guarda, Dazante, Monserrate, Pond, San Jose, and San Marcos (Grismer, 2002), as well as the Pacific Islands of Cedros and Santa Margarita (Wong, 1997). *Crotalus ruber* attains a large adult size (ca. 1200 mm snout-vent length, SVL) and occupies a wide range of habitats, including desert slopes, rocky canyons, and coastal foothills (Grismer, 2002). Habitat loss (Noss and Peters, 1995; Halama et al., 2008) and a restricted range within the United States (Beaman and Dugan, 2006) has resulted in *C. ruber* being listed as a Species of Special Concern by the state of California (Jennings and Hayes, 1994).

The southern Pacific rattlesnake (*C. o. helleri*) ranges from central California south into northern Baja California, Mexico (Grismer, 2002). Attaining an adult size (ca. 1050 mm SVL) similar to *C. ruber*, *C. o. helleri* is a habitat generalist, occupying environs ranging from pine forests above 3,000 m to beaches and sand dunes at sea-level (Stebbins, 1985). Both *C. ruber* and *C. o. helleri* are relatively understudied compared to other rattlesnake species.

Study Site

We conducted our study in the southeast portion of Chino Hills State Park (CHSP), which spans portions of Los Angeles, Orange, Riverside, and San Bernardino counties, California (33°54' N, 117°42' W). A north-south running canyon with a small perennial creek dominates the topography of the 156-ha area in which the study was confined. Dugan et al. (2008) and Figueroa et al. (2008) described the climate and general habitat features of the site.

We identified five major habitats (hereafter, macrohabitats) at the study site (Fig. 3-1): cactus, coastal sage-scrub (CSS), non-native grassland, riparian, and oak woodland (Sampson, 1985). Cactus patches of coastal pricklypear (*Opuntia littoralis*) were found exclusively on south-facing slopes. The distribution of CSS was patchy, primarily on south-facing slopes, and was usually adjacent to cactus stands. Non-native grassland was the most widespread macrohabitat, occurring extensively on hillsides and in canyon bottoms. The riparian system was largely confined to the creek channel, but penetrated into damp drainages of the grassland. Oak woodland was found primarily on north-facing slopes. The study site was almost entirely devoid of rock outcroppings, as the soil is

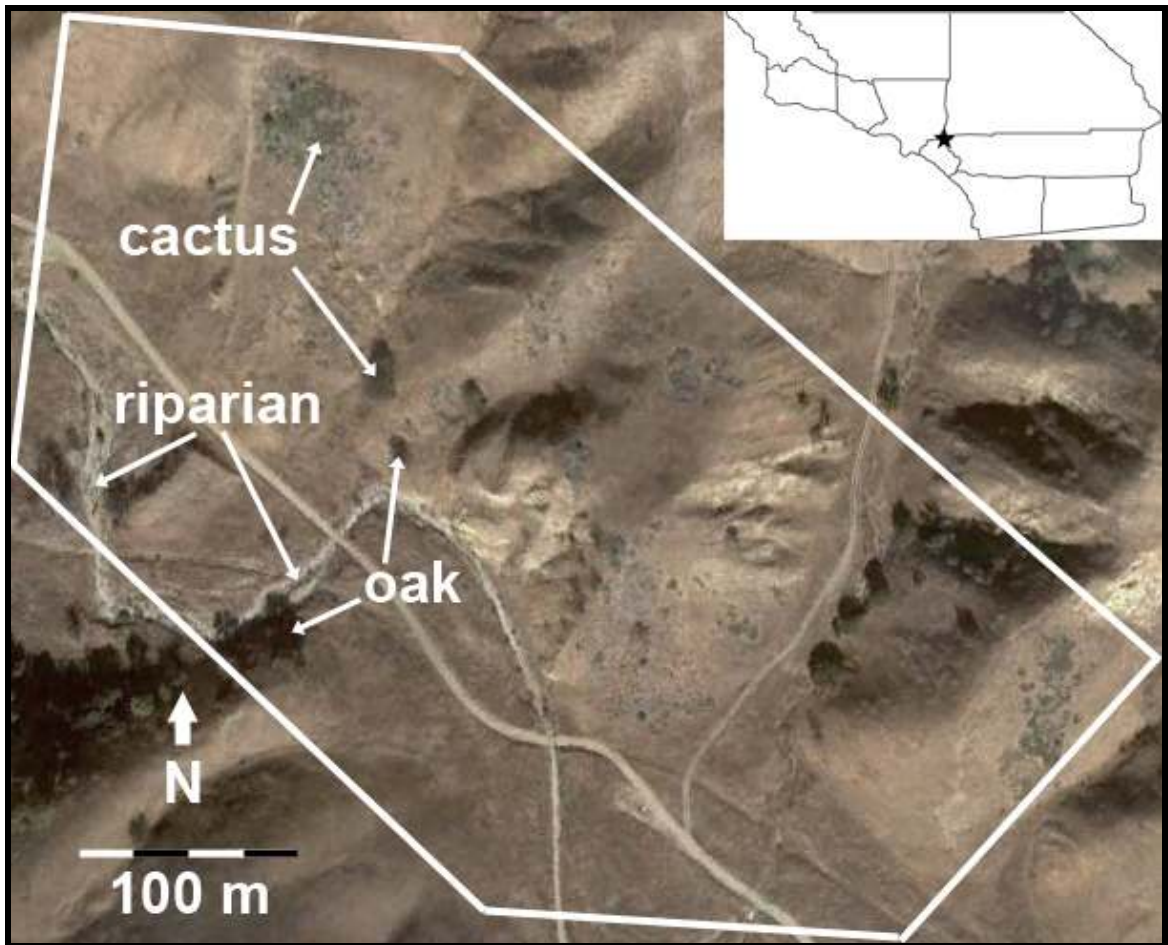


FIG. 3-1. Satellite image of study area in Chino Hills State Park, southern California, illustrating the heterogeneous distribution of the five macrohabitats. Cactus, riparian, and oak can be identified in the image, with the remainder consisting of introduced grassland and coastal sage scrub. Steep ridges are evident from shadows. Two dirt roads transect the site. Inset: study site in relation to southern California counties.

predominately clay. Sampson (1985) provided further details on relative abundance and species composition of these plant communities at CHSP.

Radiotelemetry and Mark-Recapture

We began collecting, individually marking, and implanting snakes with radio-transmitters in March 2003. All snakes captured were marked with a passive integrative

transponder (PIT) tag (AVID Identification Systems, Inc., Norco, California, USA). Our complete sample included 83 *C. ruber* (1 male, 1 female, 1 unknown-sex juveniles; 34 male, 22 female, 6 unknown-sex adults; 18 uncategorized snakes) and 110 *C. o. helleri* (12 male, 11 female, 8 unknown-sex juveniles; 33 male, 13 female, 6 unknown-sex adults; 27 uncategorized snakes). We implanted SI-2T transmitters (9 g, <5% of snake body weight; Holohil Systems Ltd., Ontario, Canada) into nine adult male *C. o. helleri* (84–103 cm snout-vent length, SVL) and nine adult male *C. ruber* (98–156 cm SVL), as described previously (Dugan et al., 2008; Chapter 2). Snakes were released at their collection site 24–36 h post-surgery. We conducted radio-tracking through March 2008 and mark-recapture through 2010. Sampling effort varied seasonally as snake activity patterns changed. Radio-tracked individuals were located 1–4 times/wk throughout the active season (March–November), and less often (bi-weekly) during the winter period (December–February). Radio-tracked snakes were lost (predation, transmitter battery failure) and replaced throughout the study, resulting in variable tracking periods (202–1762 d) for different individuals.

Macrohabitat Use

We employed two methods for analysis of macrohabitat use: compositional analysis (Aebischer et al., 1993) and logistic regression (Mertler and Vannatta, 2004). Because species differences in macrohabitat usage potentially vary seasonally, we distinguished between the active season (March–November) and the winter period (December–February; Dugan et al., 2008). Rattlesnakes at the study site retreat non-communally to burrows during much of the winter, but often emerge during warm spells, when they sometimes consume food (Dugan et al., under review; Chapter 4).

We conducted compositional analysis separately for each species to determine whether proportional usage of macrohabitat types varied from availability. This analysis used only transmittered snakes. For each snake location (or “fix”), we identified the macrohabitat occupied as cactus, coastal sage-scrub, non-native grassland, riparian, or oak woodland. To quantify availability, we recorded macrohabitat during a ground survey at each of 250 points defined by the intersections of a 25 × 25 m grid over the 156-ha study site. This area was defined by the outermost movements of all transmittered snakes. All snakes captured opportunistically were also found within this area. Compositional analysis was conducted using Adehabitat for R software 2.11.0, with alpha set at 0.05 (Calenge, 2006).

We used logistic regression to further test for species differences in macrohabitat use. Logistic regression allowed us to test the probability that we could predict which snake species occupied a given location based solely on the measured distance to the different macrohabitat types. For our models, we used five predictor variables that consisted of the measured distance (meters), obtained by measuring wheel (Fast Back, Komelon Corporation, Waukesha, Wisconsin, USA) or pacing, to each macrohabitat type (grassland, cactus, riparian, oak woodland, and CSS). This analysis allowed us to use a much larger sample of snakes, including all age classes, both sexes, and both radio-telemetered and opportunistically-collected snakes. To avoid pseudoreplication, mean distances were computed for each individual having multiple fixes. These and all statistical tests described hereafter were carried out using SPSS 13.0 for Windows (SPSS, 2003) with alpha set at 0.05.

Microhabitat Use

For each fix, we recorded occurrence in one of three microhabitats: underground (within a burrow), above-ground (on the surface), or arboreal (above the ground in vegetation). Microhabitat use varied daily (and at the same location) as much as seasonally, so we did not distinguish between seasons in our analyses. Because data were categorical (i.e., proportional), we analyzed data only from telemetered snakes that provided ≥ 7 fixes. For each snake, we computed the proportion of total fixes in each microhabitat, which reflected relative time spent in a given microhabitat but not necessarily discrete decisions about microhabitat use, since snakes often remained at one location for extended periods with multiple observations resulting at that location (Figueroa et al., 2008). Data (after arcsin transformation to better meet parametric assumptions) were subjected to a 2×3 (species \times microhabitat type) mixed analysis of variance (ANOVA; Mertler and Vannatta, 2004), with species treated as a between-subjects factor and microhabitat as a within-subjects factor. Because of non-sphericity (a multivariate assumption), Greenhouse-Geisser adjustments were applied to the degrees-of-freedom (Mertler and Vannatta, 2004). Partial eta-squared (η^2) was computed for effect size, with values of ~ 0.01 regarded small, ~ 0.06 medium, and ≥ 0.14 large (Cohen, 1988).

Thermal Resources

As ectotherms, snakes generally select preferred temperatures within a given microhabitat, so we recorded three temperature measurements at each fix when the snake was above-ground: air (T_a , 1 m above ground in shade), using a Kestrel 3000 (Nielsen-Kellerman Inc., Boothwyn, Pennsylvania, USA); shaded ground adjacent to the snake

($T_{g\text{-shade}}$, nearest shade within 2 m unless absent), using a laser thermometer (PM Plus, Raytek Corporation, Santa Cruz, California, USA); and sun-exposed ground adjacent to the snake ($T_{g\text{-sun}}$, nearest sun exposure within 2 m unless absent) via the laser thermometer. We recorded both sets of ground temperatures because snakes usually had the option of choosing either. We relied on logistic regression to compare the two species, using the three temperatures obtained from all telemetered and opportunistically-encountered snakes. To avoid pseudoreplication, mean values were entered for snakes having multiple observations.

We compared the three temperatures among the five macrohabitats using a 3×5 (temperature measures \times macrohabitat) mixed ANOVA, with temperature treated as a within-subjects factor and macrohabitat as a between-subjects factor. This analysis included data from all snake fixes. Greenhouse-Geisser adjustments were applied due to lack of sphericity. We also compared the temperature differential between $T_{g\text{-shade}}$ and $T_{g\text{-sun}}$ among the five macrohabitats using a one-way ANOVA (treating macrohabitat as a between-subjects factor). This analysis, which similarly used data from all fixes, allowed us to examine the range of proximate temperatures that a snake had access to by shuttling between sun and shade.

To further examine the snake's response to its thermal environment, we recorded the proportion (nearest 0.10) of the snake's body exposed to direct sunlight each time a snake was located above ground (c.f. Ashton 1998). We used mean values from all telemetered and opportunistically-encountered snakes. We compared the two species using an independent t -test (Zar, 1996) of arcsin-transformed data. We also computed Cohen's d as a measure of effect size (Cohen, 1988).

Activity and Temporal Resource Use

We calculated the frequencies of three behaviors recorded for each snake upon each fix: immobile (coiled and stationary), locomoting, and sexual activity (engaged in active courtship or copulation). Because data were categorical (i.e., proportional), we analyzed data only from telemetered snakes that provided ≥ 7 fixes. After arcsin transformation, data were subjected to a 2×3 (species \times behavior) mixed ANOVA, with species treated as a between-subjects factor and behavior as a within-subjects factor. Greenhouse-Geisser adjustments were applied due to lack of sphericity.

To examine seasonal differences in activity, we computed mean daily movements of snakes on a monthly basis, as described by Dugan et al. (2008). These were compared across three periods of the active season corresponding to the spring mating season of both species (March–April), the summer period (May–August), and the fall mating season of *C. o. helleri* (September–October), as documented by Dugan et al. (2008). *Crotalus ruber* has only one mating season annually (spring). This analysis included only snakes radio-tracked during 2003–2004, when the high intensity of tracking effort resulted in adequate multiple fixes each month. Mean seasonal values were computed from the monthly means of each snake (i.e., there was no pseudoreplication). These seasonal values were subjected to a 2×3 (species \times season) mixed ANOVA (after rank transformation), with species treated as a between-subjects factor and season as a within-subjects factor. The model met the assumption of sphericity. Because partial η^2 values for the main effects and interaction summed to >1.0 , we adjusted these by dividing each partial η^2 by the sum of all partial η^2 values (Dugan et al., 2008).

We also assessed the circadian activity of transmittered snakes during the active season. Snake activity was dichotomized as inactive (immobile) or active (locomoting or sexual activity), and time of day was categorized as morning (0600–1059 hr), mid-day (1100–1659 hr), or evening (1700–2159 hr). We analyzed frequency of activity (without transformation) for each time period using a 2×3 (species by time period) mixed ANOVA with Greenhouse-Geisser adjustments.

Diet

We opportunistically collected dietary data from free-ranging *C. ruber* and *C. o. helleri* at our study site during the period 2003 to 2009. Diet was determined from scat samples and feeding observations, as described in Dugan and Hayes (under review; Chapter 4). Snakes containing food boli were not palpated or forced to regurgitate food items (c.f., Macartney, 1989).

We compared the diet of the two rattlesnake species to test three hypotheses. First, we hypothesized that the two species differ in the proportions of various prey genera consumed. Second, we hypothesized that any difference in diet composition corresponds to differences in preferred habitat of the snakes, as reflected by predation disproportionately upon prey genera occurring in their preferred habitats. Third, because rattlesnakes are gape-limited predators (Shine, 1991a; Rodriguez-Robles et al., 1999), we hypothesized that *C. ruber*, as the larger species, has access to and more often consumes larger prey than *C. o. helleri*. We categorized prey genera as small (1–75 g), medium (76–275 g), or large (276–950 g). Actual prey mass was unknown, so we used the adult mass for each genus from the literature (Jameson and Peeters, 1988), as commonly done in studies of snake diets. For several genera with multiple species occurring at the study

site, we used the average mass for those species. Habitat preferences of prey genera were gleaned from the literature (M'Closkey, 1972; Meserve, 1974, 1976; Heske et al., 1984; Gillihan and Foresman, 2004). We subjected dietary data to Chi-square (χ^2) tests (when expected counts were adequate) and tests of asymmetry (either Phi [ϕ] for 2×2 or Cramer's V for larger contingency tables; Conover, 1999). Phi and Cramer's V can be interpreted as effect size, with values of ~ 0.1 deemed small, ~ 0.3 moderate, and ≥ 0.5 large (Cohen, 1988). Following Nakagawa (2004), we did not apply Bonferroni adjustments of alpha to multiple tests.

Niche Overlap

We computed Pianka's (1973) and Czekanowski's (Feinsinger et al., 1981) niche overlap indices for the major niche axes using EcoSim 7.71 (Gotelli and Entsminger, 2001). Each of these indices yields a symmetric measure of niche overlap ranging from 0 (no resources in common) to 1 (complete niche overlap). In general, low, moderate, and high niche overlap correspond to values of < 0.4 , $0.4-0.6$, and > 0.6 . Using EcoSim's null model tests, we also computed tail probabilities from randomly-assembled pseudo-communities using randomization algorithms RA2, RA3, and RA4 (Winemiller and Pianka, 1990) with 3×10^6 iterations to avoid algorithm bias (Lehsten and Harmand, 2006). We assumed equiprobable resource use for all analyses, since the two species had ready access to all resources in the relatively small study area. Interspecific competition can be inferred when niche overlap values are significantly less than expected (Gotelli and Graves, 1996). Abiotic constraints, by contrast, can impose similar patterns of resource use, resulting in niche overlap values being significantly greater than expected (Albrecht and Gotelli, 2001).

We obtained Pianka's and Czekanowski's indices for all of the major niche axes (Schoener, 1974; Saint Girons, 1978), including: macrohabitat use (five categories, from usage data as well as distances to macrohabitats); microhabitat use (three categories); thermal resources (three categories); seasonal and circadian movements (three categories each); food type (11 categories); and food size (three categories). With the exception of macrohabitat distances and diet, we restricted analysis of niche overlap to data from telemetered male snakes. Analysis of macrohabitat and dietary data included both telemetered and opportunistically-captured snakes of each species.

Results

Macrohabitat Use

We obtained data for compositional analysis from radio-tracked adult male *C. ruber* ($n = 9$ snakes, 357 fixes) and *C. o. helleri* ($n = 9$ snakes, 301 fixes). We had sufficient samples only for the active season. Figure 3-2 compares habitat use versus availability for the two species during the active season. Macrohabitat availability at the study site (based on 250 locations) consisted of 61.6% grassland, 11.6% riparian, 11.2% cactus, 10.8% coastal sage scrub, and 4.8% oak woodland. Habitat use by *C. ruber* differed significantly from random (Wilks' lambda = 0.101, $df = 4$, $P < 0.001$), with rank-order habitat use being cactus > CSS > grassland > riparian > oak woodland. This species used cactus and CSS in much greater proportion than their availability. Habitat use of *C. o. helleri* similarly differed significantly from random (Wilks' lambda = 0.133, $df = 4$, $P = 0.001$), with rank-order habitat use being riparian > cactus > grassland > CSS > oak woodland. Riparian was used in far greater proportion than its availability. Both species used oak woodland less than its availability.

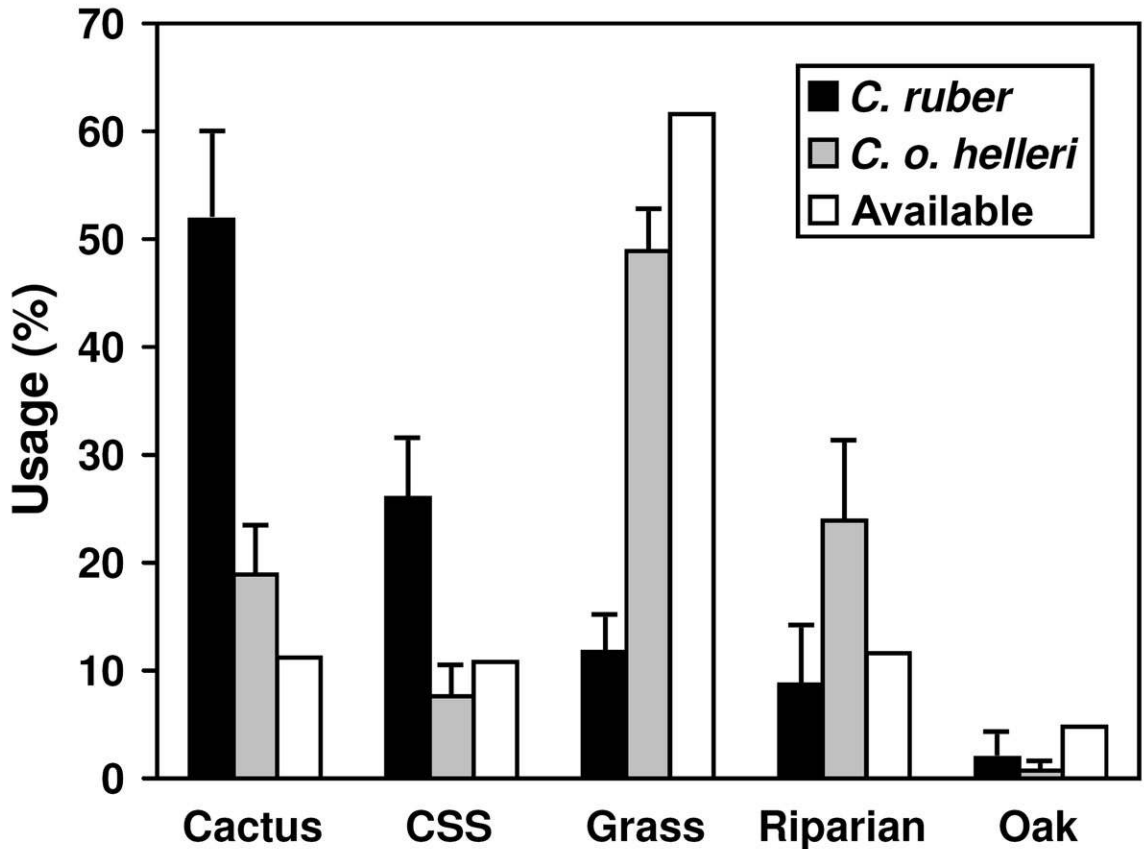


FIG. 3-2. Spatial axis: Macrohabitat availability versus macrohabitat use (mean percentage \pm 1 SE) by radio-telemetered adult male *Crotalus ruber* ($n = 9$) and *C. o. helleri* ($n = 9$) during the active season (March–November).

To compare species differences by logistic regression, we obtained macrohabitat data (distances to each macrohabitat type) from 57 *C. ruber* ($n = 9$ transmittered and 48 opportunistically-encountered) and 70 *C. o. helleri* ($n = 9$ and 61, respectively) during the active season, and from 13 *C. ruber* ($n = 5$ and 8, respectively) and 12 *C. o. helleri* ($n = 4$ and 8, respectively) during the winter period. Many of the opportunistically-encountered snakes were recorded more than once, and included snakes of both sexes and size classes. The number of fixes per animal used to compute average values varied from one (64.8% of all snakes) to 63 in the active season, and from one (50.0% of all snakes) to 16 during

winter. Logistic regression confirmed that *C. ruber* and *C. o. helleri* used different macrohabitats during the active season ($\chi^2 = 90.88$, $df = 5$, $P < 0.001$, $-2 \log \text{likelihood} = 83.85$, Nagelkerke $R^2 = 0.68$; Fig. 3-3). The model successfully predicted the correct snake species for 87.4% of all locations (*C. ruber* = 87.7%; *C. o. helleri* = 87.1%). Distances to cactus and grassland were the only two significant predictors of differences between the two species ($P = 0.021$ and 0.002 , respectively; log-odds ratios = 0.95 and 1.13, respectively), with *C. ruber* averaging closer to cactus and *C. o. helleri* closer to grassland. The two species also used different macrohabitats during the winter period ($\chi^2 = 24.58$, $df = 5$, $P < 0.001$, $-2 \log \text{likelihood} = 10.03$, Nagelkerke $R^2 = 0.84$), with the model successfully predicting snake species for 92.0% of all locations (*C. ruber* = 100.0%; *C. o. helleri* = 83.3%). Because of the smaller sample size, no single predictor proved to be significant, though the log-odds ratio (i.e., effect size) was largest for distance to grassland (1.32; compare with the active season model above). Macrohabitat use within species was similar during the active and winter seasons, but because our samples included both independent and related data, we did not compare seasonal usage statistically.

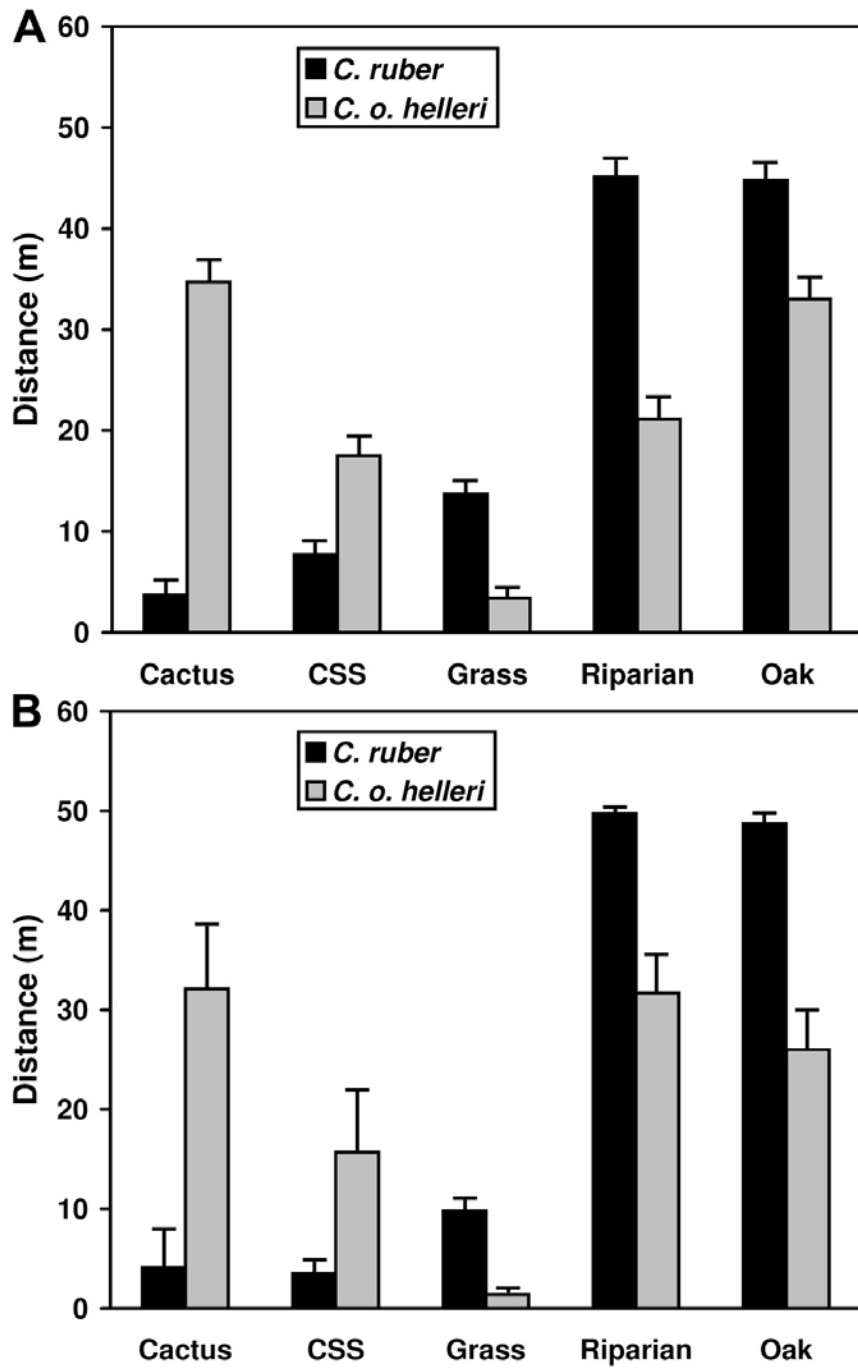


FIG. 3-3. Spatial axis: Macrohabitat characteristics (distances to nearest macrohabitat type, mean \pm 1 SE) of individual locations used by radio-telemetered and opportunistically encountered *Crotalus ruber* ($n = 57$) and *C. o. helleri* ($n = 70$) during the (A) active season (March–November) and (B) winter (December–February).

Microhabitat Use

For proportional data on snake location relative to the ground surface, we analyzed data only from telemetered subjects (*C. ruber*: $n = 9$ adult males, 17–99 fixes per snake; *C. o. helleri*: $n = 7$ adult males; 20–103 fixes per snake). Repeated-measures ANOVA indicated that microhabitat use was similar for the two species ($F_{1,0,14.2} = 0.21$, $P = 0.65$, partial $\eta^2 = 0.01$) and that no interaction existed between species and microhabitat type, though the effect size was moderate ($F_{1,0,14.2} = 1.73$, $P = 0.21$, partial $\eta^2 = 0.11$). However, snake use differed significantly among the three microhabitats ($F_{1,0,14.2} = 43.89$, $P < 0.001$, partial $\eta^2 = 0.76$). Bonferroni pairwise comparisons confirmed similar percentages (mean \pm 1 SE pooled for both species) of below-ground ($53.1 \pm 3.9\%$) and above-ground (46.4 ± 4.0) usage, and these significantly exceeded arboreal use ($0.4 \pm 0.3\%$). Including snakes of all sizes in the present study, we observed snakes in arboreal positions on just four of 1,121 fixes with microhabitat data; these involved one adult *C. ruber* and three adult *C. o. helleri* (c.f., Figueroa et al., 2008).

Thermal Resources

For thermal attributes of positions occupied by snakes, we obtained data from 49 ($n = 9$ transmittered and 40 opportunistically-encountered) *C. ruber* and 78 *C. o. helleri* ($n = 9$ and 66, respectively). Logistic regression using mean values for individual snakes revealed that *C. ruber* and *C. o. helleri* occupied locations which differed significantly in their thermal attributes ($\chi^2 = 15.26$, $df = 3$, $P = 0.002$, $-2 \log \text{likelihood} = 154.12$, Nagelkerke $R^2 = 0.15$; Fig. 3-4). The model successfully predicted the correct snake species for 65.4% of all locations (*C. ruber* = 34.7%; *C. o. helleri* = 84.6%), with fixes

predicted with much better success for *C. o. helleri*. Ground temperature in the sun ($T_{g\text{-sun}}$) was the single significant predictor of differences between the two species ($P = 0.002$; log-odds ratio = 1.11). Microhabitats occupied by *C. ruber* had warmer ground available from solar radiation than those occupied by *C. o. helleri* (Fig. 3-4).

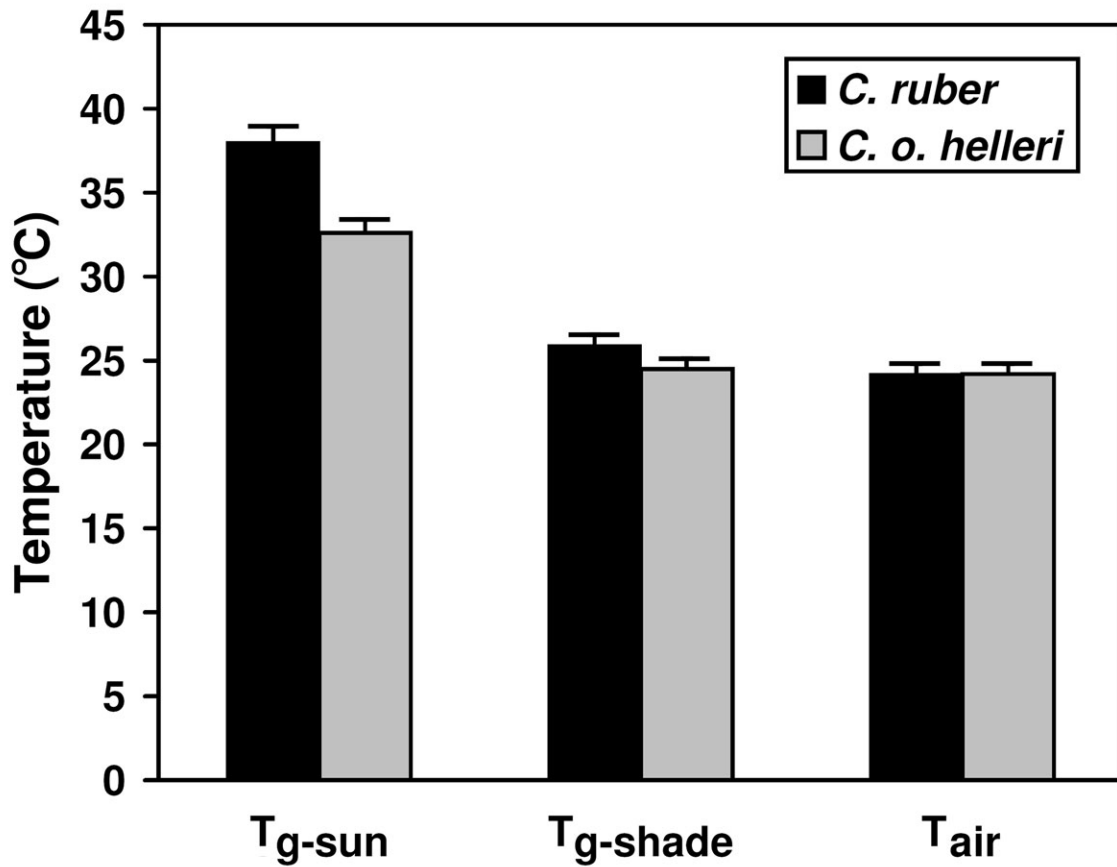


FIG. 3-4. Thermal axis: thermal attributes (mean \pm 1 SE) of locations occupied by radio-telemetered and opportunistically encountered *Crotalus ruber* ($n = 49$) and *C. o. helleri* ($n = 78$), as measured by temperature of the ground in the sun ($T_{g\text{-sun}}$), ground in the shade ($T_{g\text{-shade}}$), and ambient air temperature (T_{air}).

Differences among the three temperatures varied among the five macrohabitats ($n = 316$ cactus, 123 CSS, 234 grassland, 93 riparian, and 11 oak woodland), as reflected in the weak but significant interaction of the 3×5 (temperature measures \times macrohabitat) ANOVA ($F_{5.5,1063.7} = 8.40$, $P < 0.001$, partial $\eta^2 = 0.04$). This effect resulted because the largest difference between $T_{g\text{-sun}}$ and other temperatures (T_a , $T_{g\text{-shade}}$) was 9.4–12.8°C in all macrohabitats except oak woodland, for which the difference was only 2.3°C. Thus, snake locations in oak woodland had much more even temperatures, presumably due to the overhead canopy blocking direct sunlight.

The majority of fixes (79.6% of 794 records) showed a difference in temperature between $T_{g\text{-sun}}$ and $T_{g\text{-shade}}$. The mean temperature difference of 10.5°C indicated the remarkable ease with which snakes could thermoregulate via minor movements (<1–2 m) and/or postural adjustments (see below) to alter body exposure to solar radiation. The one-way ANOVA revealed differences in the ground temperature differential among the five macrohabitats ($F_{4,772} = 9.13$, $P < 0.001$, $\eta^2 = 0.05$), with the cactus differential being greatest ($12.3 \pm 0.5^\circ\text{C}$) and oak least ($2.3 \pm 1.0^\circ\text{C}$).

The two species differed in the percentage of body exposed to direct sunlight ($t = 2.24$, $df = 1$, $P = 0.027$, Cohen's $d = 0.49$), with *C. ruber* ($41.3\% \pm 4.1\%$, $n = 74$) exhibiting greater exposure than *C. o. helleri* ($23.6\% \pm 4.0\%$, $n = 83$). Among all snake locations recorded ($n = 749$, both species pooled), 28.7% consisted of snakes in partial sunlight (i.e., 10–90% of body).

Activity and Temporal Resource Use

To compare general levels of activity between species, we analyzed proportional data for immobile, locomoting, and sexual behaviors only from transmittered *C. ruber* (n

= 8; 9–60 fixes per individual) and *C. o. helleri* ($n = 9$; 7–60 fixes per individual).

Repeated-measures ANOVA showed a significant interaction between species and behavior ($F_{1,1,16,1} = 5.86$, $P = 0.026$, partial $\eta^2 = 0.28$). Among the three behaviors, *C. ruber* was inactive 1.2-fold more frequently than *C. o. helleri*, whereas *C. o. helleri* engaged in locomotion 1.7-fold and sexual activity 2.3-fold more frequently than *C. ruber* (Fig. 3-5).

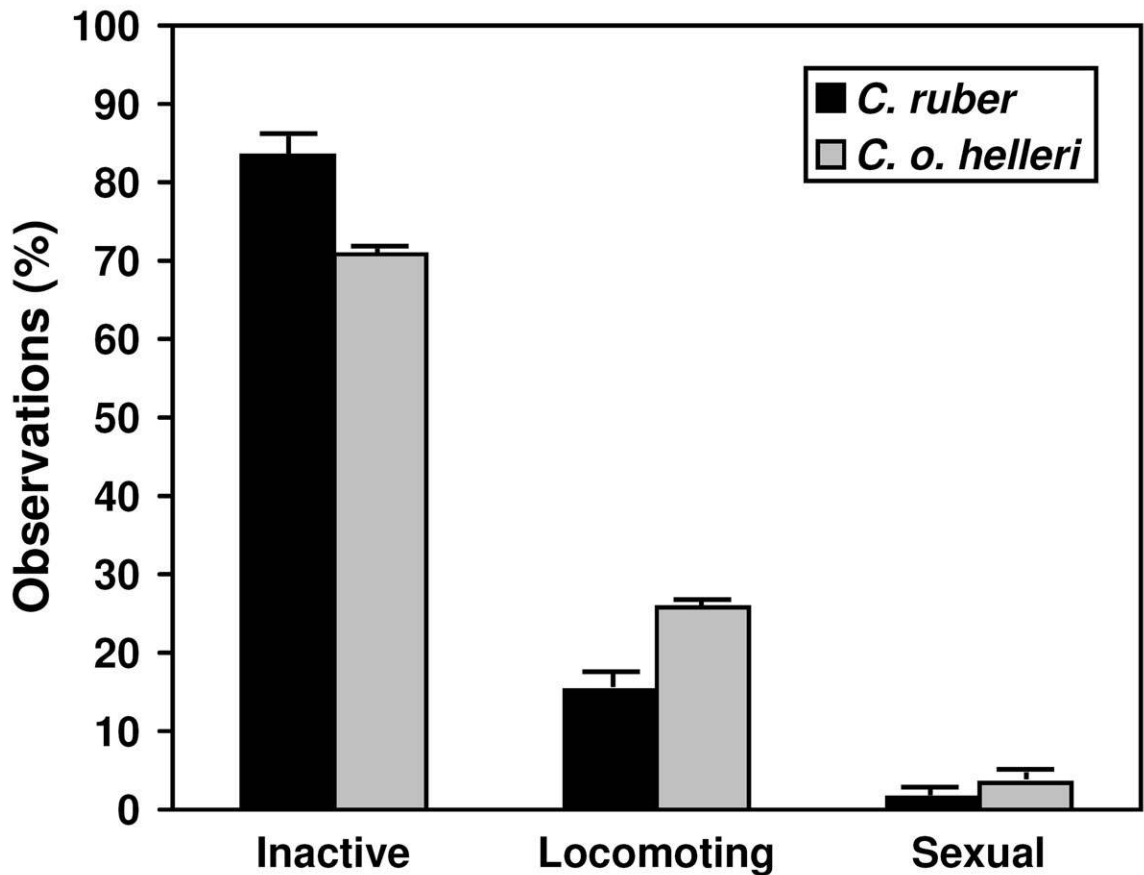


FIG. 3-5. Temporal axis: Comparison of activities exhibited (percentage of observations, mean \pm 1 SE) by radio-telemetered adult male *Crotalus ruber* ($n = 8$) and *C. o. helleri* ($n = 9$).

Transmittered snakes with sufficient mean daily movement data (six *C. ruber* and six *C. o. helleri*) revealed significant differences between species ($F_{1,10} = 12.99$, $P = 0.005$, adjusted partial $\eta^2 = 0.51$) and in seasonality of activity ($F_{2,20} = 11.67$, $P < 0.001$, adjusted partial $\eta^2 = 0.48$), with no interaction between these variables ($F_{2,20} = 0.12$, $P = 0.89$, adjusted partial $\eta^2 = 0.01$). *Crotalus o. helleri* exhibited higher levels of activity than *C. ruber* in all three seasons, and both species were more than two-fold more active in spring than during summer (Fig. 3-6). However, the lack of an interaction confirmed similar seasonal levels of activity, and presumably similar seasonal use of resources, by the two species.

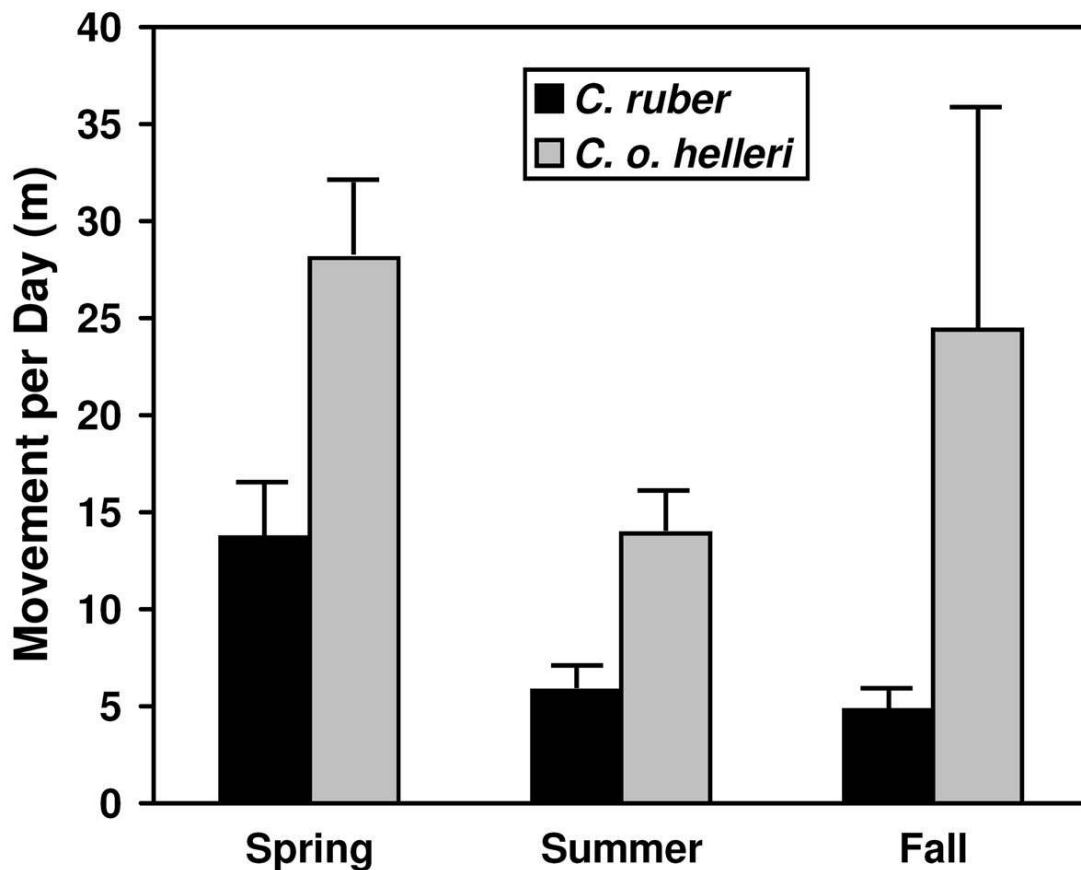


FIG. 3-6. Temporal axis: Seasonal variation of movements (mean \pm 1 SE) by radio-telemetered adult male *Crotalus ruber* ($n = 6$) and *C. o. helleri* ($n = 6$).

Transmittered snakes with adequate observations of circadian activity during the active season (eight *C. ruber* and nine *C. o. helleri*) showed no differences between species ($F_{1,15} = 1.39$, $P = 0.26$, partial $\eta^2 = 0.09$) or among the morning, mid-day, and evening time periods ($F_{1,4,20.5} = 0.72$, $P = 0.45$, partial $\eta^2 = 0.05$; Fig. 3-7). The lack of an interaction ($F_{1,4,20.5} = 0.55$, $P = 0.52$, partial $\eta^2 = 0.04$) confirmed similar circadian patterns of activity by the two species.

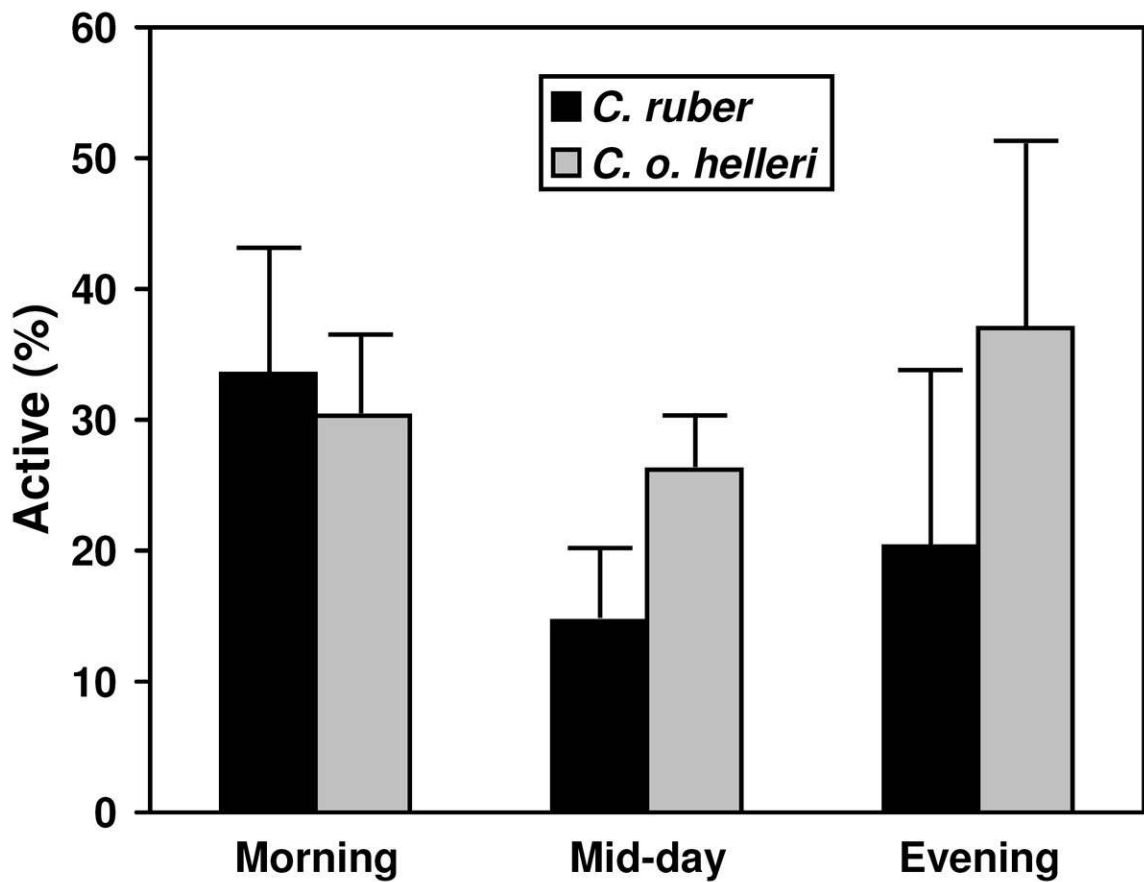


FIG. 3-7. Temporal axis: Circadian activity (percent of observations, mean \pm 1 SE) of radio-telemetered and opportunistically encountered *C. ruber* ($n = 8$) and *C. o. helleri* ($n = 9$) in Chino Hills State Park.

Diet

Of the 83 individual *C. ruber* marked at our site, 14 (18.1%) yielded 21 prey items identifiable to genus (Table 3-1). These were from 10 male and four female adults (735–1090 mm SLV; one neonate containing an unidentified rodent was excluded). We obtained nineteen (90.5%) prey records from fecal contents and two (9.5%) from observations of snakes feeding in the field. Four snakes contained multiple prey items (26.7%), with two containing two mammals of different species and two containing three mammals of different species. Identifying multiple prey was possible from feces only if two or more different prey species were found, leading to underestimation of snakes containing multiple prey. Among the prey items of *C. ruber*, we identified 21 mammals (100%) and no reptiles (c.f., Dugan and Hayes, under review; Chapter 4). The 21 mammals, all identifiable to genus, were distributed among six genera (Table 3-1): *Microtus* (4.8%); *Neotoma* (52.4%); *Onychomys* (4.8%); *Otospermophilus* (4.8%); *Peromyscus* (14.2%); and *Sylvilagus* (19.0%).

TABLE 3-1. Number of prey items per taxon (mass from Jameson and Peeters, 1988) consumed by sympatric *Crotalus ruber* and *C. oreganus helleri* in Chino Hills State Park, California, including frequency (*n*), Phi test of asymmetry (*P*-value) for snake species differences, and habitat preferences of prey.

Prey Taxon (mass)	<i>C. ruber</i> <i>N</i>	<i>C. o. helleri</i> <i>N</i> ^a	<i>P</i>	Preferred Habitat
Mammals				
<i>Chaetodipus</i> (15 g)	0	7 (5)	0.019	Grasslands ^f
<i>Microtus</i> (60 g)	1	1		Grasslands ^c
<i>Neotoma</i> (275 g)	11	1	<0.001	Coastal sage scrub, cactus ^{d,f}
<i>Onychomys</i> (23 g)	1	0		Not determined
<i>Otospermophilus</i> (475 g)	1	7	0.081	Grasslands, riparian ^g
<i>Peromyscus</i> (28 g)	3	5 (2)	0.86	No preference ^e
<i>Reithrodontomys</i> (12 g)	0	2 (1)		Grasslands ^{d,f}
<i>Sorex</i> (12 g)	0	2 (1)		Grasslands ^b
<i>Sylvilagus</i> (950 g)	4	2	0.16	No preference ^g
<i>Thomomys</i> (154 g)	0	3		No preference ^g
Reptiles				
<i>Uta stansburiana</i> (8 g)	0	1		No preference ^g
Totals	21	31		

^a Values in parentheses for adult snakes only (after exclusion of prey from neonate *C. o. helleri*); significance was similar after retesting.

^b Gillihan and Foresman, 2004

^c Heske et al., 1984

^d M²Closeky, 1972

^e Meserve, 1974

^f Meserve, 1976

^g Dugan and Hayes, pers. obs.

Of the 110 *C. o. helleri* we marked at our site, 24 (21.8%) yielded 31 partially identifiable prey (Table 3-1). These were from three male, one female, and two unknown-sex neonates (298–320 mm SVL), and from 11 male, 1 female, and 5 unknown-sex adults (570–930 mm SVL). The higher proportion of dietary items from juveniles of *C. o. helleri* compared to *C. ruber* was significant (22.6% and 0%, respectively; $\phi = 0.33$, $P = 0.019$), requiring consideration of this bias in the analyses that follow. We procured 29 (93.5%) prey records from fecal samples and two (6.5%) from observations of snakes feeding in the field. Seven snakes contained multiple prey items (29.2%), with six having

consumed two mammals of different species, and one containing a mammal and a lizard. Among the 31 prey items identified, 30 (96.8%) were mammals and one (3.2%) was a lizard. The mammals were widely distributed among nine genera: *Chaetodipus* (22.6%); *Microtus* (3.2%); *Neotoma* (3.2%); *Peromyscus* (16.2 %); *Reithrodontomys* (6.5%); *Otospermophilus* (22.6%); *Sorex* (6.5%); *Sylvilagus* (6.5%); and *Thomomys* (9.7%). All six neonates contained mammal food (seven items in all), which was surprising since younger snakes generally feed on lizards (LaBonte, 2008; Mackessy, 1988), and lizards abound at the study site (Figueroa et al., 2008). The single lizard record was a *Uta stansburiana* in a 605 mm SVL male.

For the five prey species represented by $N \geq 5$ samples, *C. ruber* and *C. o. helleri* differed significantly in diet composition ($\chi^2 = 20.89$, $df = 4$, $P < 0.001$, Cramer's $V = 0.71$; see Table 3-1). The difference corresponded to habitat preferences of the two species. *Crotalus ruber* preyed significantly more often than *C. o. helleri* on wood rats (*Neotoma* spp.; $\phi = 0.57$, $P < 0.001$), which occur primarily in *C. ruber*'s preferred habitat of cactus and CSS. *Crotalus o. helleri* preyed more often than *C. ruber* on pocket mice (*Chaetodipus* spp.; $\phi = 0.33$, $P = 0.019$) and California ground squirrels (*Otospermophilus beecheyi*; $\phi = 0.24$, $P = 0.081$), which occur primarily in *C. o. helleri*'s preferred grassland habitat. Both rattlesnake species consumed cottontail rabbits (*Sylvilagus* spp.; $\phi = 0.19$, $P = 0.16$) and deer mice (*Peromyscus* spp.; $\phi = 0.03$, $P = 0.86$), which occupy a broad range of habitats, with similar frequency. The significance of differences was unchanged when data were reanalyzed after excluding neonate *C. o. helleri*. Diet breadth was greater for *C. o. helleri* (nine mammal and one reptile genera) than *C. ruber* (six mammal genera).

Prey size class (small, medium, and large) also differed significantly among the two snake species ($\chi^2 = 10.21$, d.f. = 2, $P = 0.006$, Cramer's $V = 0.44$; Fig. 3-8). *Crotalus ruber* most often procured medium-sized prey species, whereas *C. o. helleri* most frequently consumed smaller prey species. Neonates of *C. o. helleri* consumed only small rodents (*Chaetodipus*, *Peromyscus*, *Reithrodontomys*, *Sorex*), which contributed to the prey size disparity. However, the prey size class difference between species remained significant even after excluding the neonates ($\chi^2 = 6.48$, df = 2, $P = 0.039$, Cramer's $V = 0.38$). Large prey species were consumed in similar proportions by both snake species, representing approximately 25% of each predator's diet. However, the primary source of large prey records differed for each species, with *C. ruber* preying more often on rabbits, and *C. o. helleri* consuming California ground squirrels with greater frequency.

Niche Overlap

We evaluated 11 data sets for niche overlap, including: year-round macrohabitat use (proportional data from all transmitterd snakes: nine *C. ruber*, nine *C. o. helleri*) and distances to macrohabitats during active and winter seasons (mean values for all transmitterd and opportunistically-encountered snakes); microhabitat use (species means from all transmitterd snakes); thermal resources (species means of all transmitterd snakes); seasonality of movements (species means of most transmitterd snakes: six *C. ruber*, six *C. o. helleri*); circadian activity (species means of most transmitterd snakes: eight *C. ruber*, nine *C. o. helleri*); food type and food size (from 15 *C. ruber*, 24 *C. o. helleri* specimens). Because of age-class bias in dietary samples, we computed additional indices after excluding from analysis the prey obtained from neonate *C. o. helleri*.

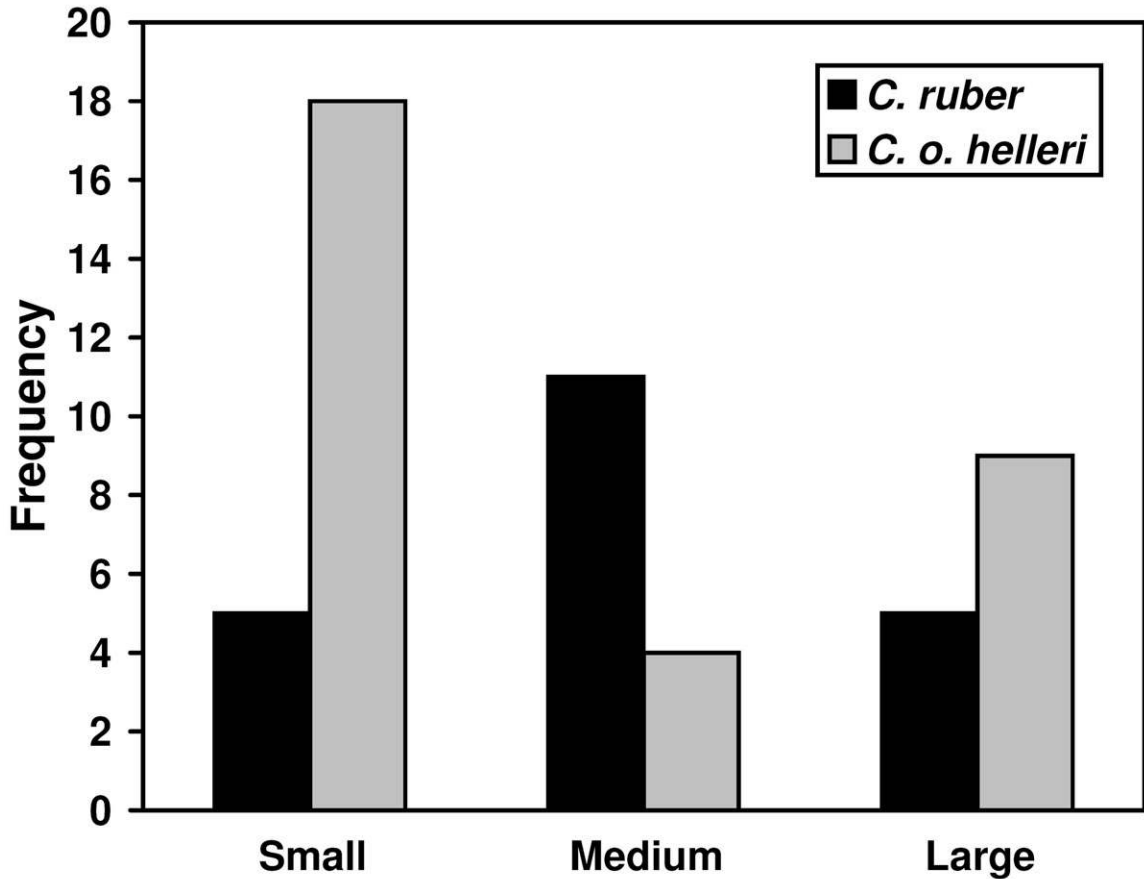


FIG. 3-8. Dietary axis: Prey size class utilization by radio-telemetered, opportunistically encountered, and road-killed *Crotalus ruber* and *C. o. helleri*. Prey size classes are based on the adult size of prey species (see Methods).

The three algorithms used for the Monte Carlo simulations of randomly-assembled communities gave very similar results, particularly RA3 and RA4. Compared to the others, RA2 produced larger differences between observed and expected values for macrohabitat (proportional usage), macrohabitat (distances for Czekanowski's index), thermal, temporal, and prey type niche axes, and smaller differences for macrohabitat (distances for Pianka's), microhabitat, and prey size niche axes. We report only RA3 results in Table 3-2, which conserves niche breadth for both species in contrast to RA2, and is more likely to detect non-random niche overlap than RA4 (Winemiller and Pianka,

1990). In our analyses, the RA3 results provided conclusions consistent with those derived from the other algorithms.

Pianka's and Czekanowski's indices yielded different interpretations for two niche comparisons. Pianka's index was more likely to find non-randomness for thermal resources and for prey size when all snakes were included, whereas Czekanowski's detected non-randomness only for prey size when analysis was restricted to adult snakes (Table 3-2). Czekanowski's index also showed a bias toward moderate values relative to Pianka's index.

Niche overlap varied substantially among the niche axes, with lowest values for diet (food type: 0.28–0.32), moderate overlap for macrohabitat (year-round usage: 0.48–0.56), and high overlap for all other resources (Table 3-2). However, the only evidence for niche partitioning between the two snake species was in prey size ($P < 0.001$), for which observed index values were significantly less than expected in the null model pseudo-communities. Index values for temperature were greater than expected ($P < 0.001$; the P -value for less than expected is shown in Table 3-2), suggesting that abiotic constraints impose similarity in thermal niche use by the two species.

TABLE 3-2. Pianka's and Czekanowski's niche overlap values for major niche axes resulting from pairwise comparisons between sympatric *Crotalus ruber* and *C. oreganus helleri*.

Niche Axis	Pianka's Index ^b			Czekanowski's Index ^b		
	Obs	Exp	$P_{obs<exp}$	Obs	Exp	$P_{obs<exp}$
Space: macrohabitat (% usage)	0.56	0.58	0.564	0.48	0.53	0.468
Space: macrohabitat (distances, active season)	0.76	0.70	0.586	0.62	0.59	0.565
Space: macrohabitat (distances, winter season)	0.79	0.65	0.724	0.62	0.53	0.730
Space: microhabitat	0.96	0.64	0.836	0.85	0.58	0.836
Temperature	1.00	0.97	>0.999	1.00	0.91	0.832
Temporal: seasonal movements	0.91	0.88	0.497	0.81	0.77	0.499
Temporal: circadian activity	0.94	0.94	0.666	0.83	0.84	0.504
Diet: prey type, all snakes	0.28	0.40	0.307	0.32	0.37	0.323
Diet: prey type, adults only ^a	0.28	0.38	0.348	0.30	0.36	0.234
Diet: prey size, all snakes	0.67	0.81	<0.001	0.61	0.72	0.335
Diet: prey size, adults only ^a	0.75	0.87	0.327	0.64	0.76	<0.001

^a Values after exclusion of prey from neonate *C. o. helleri*.

^b Expected values based on Monte Carlo simulations of randomly-assembled communities (3×10^4 iterations) using randomization algorithm 3 (RA3); bold font indicates significant non-random structure, with $P_{obs<exp} \leq 0.05$ indicating niche partitioning greater than expected, and $P_{obs<exp} \geq 0.95$ indicating biological properties that impose similarity.

Discussion

Niche separation between closely-related sympatric species can be achieved via differences in food (type or size) or in use of spatial (macrohabitat or microhabitat), temporal (diel or seasonal activity patterns), or thermal resources (Schoener, 1974; Saint Girons, 1978). The present study uncovered significant quantitative differences between the sympatric rattlesnakes *C. ruber* and *C. o. helleri* in most of the niche aspects we measured. The two species differed in their use of space at the macrohabitat (but not microhabitat) level, use of thermal resources, activity level, phenology of reproduction (the latter analyzed in more detail by Dugan et al., 2008), and diet (both composition and prey size). However, null models examining overlap in the use of these resources

suggested that niche partitioning exists only for the dietary axis, and this was apparent only for prey size. Here, we argue that niche separation between these two rattlesnake taxa has probably resulted largely from non-competitive mechanisms. If niche partitioning exists, we believe it occurs subtly along more than one niche axis, but probably more so via differential habitat use than other axes. We suggest that dietary differences reflect habitat preference and body size-dependent differences between the two snake species. Although these sympatric rattlesnakes may be similar to other vipers and most vertebrates in partitioning habitat (Luiselli, 2006a,b; Luiselli et al., 2007), the evidence for demonstrating this remains elusive.

In the sections that follow, we discuss the relative importance of each axis for niche separation between these two rattlesnake species. Although we have not demonstrated the existence or consequences of interspecific competition, we assume that food (rodent) availability—a limited resource exploited by both species—limits the population of each species. Accumulating evidence suggests that reproduction by rattlesnakes is constrained by food availability (Beaupre, 2008; Nowak et al. 2008; Taylor and DeNardo, 2010). We also acknowledge that equalizing or neutral mechanisms, rather than or in addition to niche or stabilizing mechanisms (i.e., niche partitioning), can promote coexistence of similar species (e.g., Adler et al., 2007; Cadotte, 2007; Chesson, 2000; Vergnon et al., 2009).

Macrohabitat Use

We found significant differences between the two species in use of macrohabitats, consistent with studies of sympatric vipers in western (Pough, 1966; Reynolds and Scott, 1982; Mendelson and Jennings, 1992; Beck, 1995) and eastern (Reinert, 1984; Waldron

et al., 2006; Steen et al., 2007) North America, and in Europe (Monney, 1996; Saint Girons, 1975; Luiselli et al., 2007), Africa (Luiselli et al., 2006b), and tropical Asia (Orlov, 1997; Luiselli, 2006a). Our study site comprised a heterogeneous mosaic of macrohabitats. Comparisons of the two species revealed several general trends at our site. First, *C. ruber* clearly selected cactus and CSS habitats relative to availability. These dense macrohabitats were almost exclusively located on warm south-facing slopes. Second, *C. o helleri* preferentially selected riparian (compositional analysis of usage) and grassland (logistic regression of distances) habitats, but also used cactus greater than availability (compositional analysis). The majority of riparian sites were in low-lying flat areas of the study site, while grasslands were present on both south- and north-facing slopes. Third, both species appeared to avoid oak woodlands, using it at a much lower frequency than availability. Because oak woodlands contain ample prey resources (e.g., *Neotoma* sp., *Otospermophilus*, and *Peromyscus californicus*; M'Closkey, 1972; Meserve, 1974, 1976; Dugan, pers. obs.), we were surprised that neither species used the oak woodland with any regularity. The ability to thermoregulate may lead snakes to avoid oak habitat, where the temperature differential at above-ground locations is least conducive to behavioral thermoregulation. Finally, we found no difference in habitat preferences between the active season and winter, suggesting consistent habitat use year-round. Our analyses based on both radiotracked snakes (compositional analysis, using adult males only) and all snakes encountered (logistic regression) suggest that the habitat use differences between species can be generalized to both sexes and all age classes.

Klauber (1972:540,544) provided habitat association data with encounters of *C. ruber* and *C. o. helleri* on roads primarily within San Diego County, California. For seven

habitat categories (excluding captures on the desert slope where *C. o. helleri* is absent), we computed Pianka and Czekanowski's index values (0.60 and 0.49, respectively) that were very similar to those obtained at our study site (0.56 and 0.48, respectively). Like our overlap values, the differences from expected values, determined by pseudo-community simulations, were not significant. Klauber found *C. ruber* primarily in heavy brush-chaparral and rocky areas (50.8% of 23.7% of 59 records, respectively), and *C. o. helleri* mostly in agricultural (including orchards), grassland, and heavy brush-chaparral areas (17.6%, 36.3%, and 20.9% of 91 records, respectively). Halama et al. (2008), using a GIS model for occurrence, similarly found preference of *C. ruber* for rocky habitats. Rocks were essentially absent from our study site, but our findings suggest that cactus has been overlooked as a preferred habitat of *C. ruber* (but see Brown et al., 2008). Nevertheless, we conclude that differences in macrohabitat preferences between these two species likely occur on a broad geospatial scale.

We saw no evidence of interspecific interference competition (aggression or predation), as this is absent to extremely rare among rattlesnakes (cannibalism has been reported; Klauber, 1972; Mociño-Deloya, 2009). Indeed, we occasionally observed close spatial tolerance of the two species (within 2–3 m of each other). We suspect that rattlesnakes rely heavily on chemosensory cues for locating appropriate habitat (Bevelander et al., 2006; Theodoratus and Chiszar, 2000), and they might incorporate both conspecific and heterospecific odors in their decision-making. Laboratory experiments could shed light on this possibility.

Finally, we suggest that the cactus macrohabitat at our site afforded a selective advantage to *C. ruber* in terms of protection from predators. Mortality rates of

telemetered snakes differed for the two species, with a higher level of predation on transmittered adult *C. o. helleri* compared to *C. ruber* (Dugan et al., unpubl. data). Although *C. o. helleri* frequently used cactus, all of the predation events we recorded for the species occurred in either grassland or riparian macrohabitats.

Microhabitat Use

We found substantial niche overlap in microhabitat use between adult male *C. ruber* and *C. o. helleri*, with indices of 0.85–0.96. Both rattlesnake species used above-ground and subterranean microhabitats similarly, often moving between the two microhabitats within a 24-h period. Arboreal habitat use was infrequent by both species (0.4% of all observations). Although rare in adult rattlesnakes (Klauber, 1972), arboreal behavior has been recorded in numerous species, including *C. catalinensis* (Grismer, 2002; Martins et al., 2008), *C. durissus* (Santos et al., 2010), *C. horridus* (Rudolph et al., 2004; Sajdak and Bartz, 2004), *C. lepidus klauberi* (Rossi and Feldner, 1993), *C. o. helleri* (Figueroa et al., 2008), *C. tigris* (Pavlik, 2007), and *C. w. willardi* (Rossi and Feldner, 1993). However, use of arboreal microhabitats appears to be more common in juvenile and subadult rattlesnakes (Rudolph et al., 2004; Cobb et al., 2005; Figueroa et al., 2008). Radiotracked neonate *C. o. helleri* at our study site used arboreal habitat much more frequently (10.4% of observations) than adults (Figueroa et al., 2008). We suggested this difference relates to the ontogenetic change in foraging behavior of this species (Figueroa et al., 2008), as young *C. o. helleri* prey largely on lizards and transition to mammalian prey as adults (Mackessey, 1988; LaBonte, 2008). We frequently observe lizards using arboreal microhabitats at our study site. However, neonate *C. o. helleri* at our study site frequently consume rodents, which also ascend into

the vegetation (Laakkonen, 2003). Arboreality in neonates might also confer antipredatory benefits.

Thermal Resources

We found broad thermal niche overlap between the two rattlesnake species. Although *C. ruber* occupied microhabitats with slightly warmer ground temperatures in the sun than *C. o. helleri*, other temperatures (air and shaded ground) were similar. The two species showed complete niche overlap of thermal resources, with index values of 1.00. Because our sample included both sexes and all age classes, the results can be generalized at the species level. Intraspecifically, however, we would expect gravid females to select warmer temperatures than males (Charland and Gergory, 1990; Reinert and Zappalorti, 1988; Reinert, 1993; Gardner-Santana and Beaupre, 2009; Harvey and Weatherhead, 2010).

The different habitats at our site presented similar thermal resources, with the exception of oak woodlands offering cooler thermal conditions and less temperature differential, presumably due to shade from the canopy. Considering the broad range of temperatures available to a snake in close proximity to its position (often a 10°C difference between moving into nearby sun or shade), and the ease of thermoregulation by positioning a variable portion of its body in direct sunlight (i.e., regional heterothermy; Dorcas and Peterson, 1997; Dorcas and Roark, 2000; Ashton, 1998), it seems highly unlikely that the two species would reduce competition by partitioning thermal resources to any extent. Nevertheless, some sympatric non-viperid snake species do appear to partition thermal resources (Fukada, 1992; Mushinsky et al., 1980; Tanaka and Ota, 2002).

Among all snake locations recorded, a large percentage (28.7%) consisted of snakes in partial sunlight (i.e., 10–90% of body), suggesting a major role of regional heterothermy in thermoregulation. The significant difference between the two species in sunlight exposure suggests that *C. ruber* may utilize this strategy (regional heterothermy) to a greater extent than *C. o. helleri*. However, the difference may reflect instead the larger body size of *C. ruber* (with a portion of body more likely to be in partial sunlight) or differential habitat use (with more partial sunlight available in its preferred habitat).

Temporal Resources

Competitors often limit the effects of competition by accessing or utilizing common resources at different times or seasons. Adult male *C. o. helleri* undertook more extensive movements than *C. ruber* during all seasons, and exhibited more frequent locomoting and sexual behaviors. We attribute these differences to *C. o. helleri* having a bi-modal mating season (both spring and fall) compared to the spring-only mating season of *C. ruber* (Dugan et al., 2008). Male rattlesnakes routinely undertake prolonged mate searches during periods of breeding (Duvall et al., 1992; Aldridge et al., 2002). In spite of the quantitative differences, the patterns of seasonal and circadian activity were similar for the two species, with index values (0.81–0.94) revealing extensive niche overlap. Luiselli (2006a) concluded that sympatric snakes rarely partition the temporal niche axis.

Dietary Resources

Attributes of trophic resources such as prey class (e.g., reptile versus mammal), body size, diversity, abundance, and seasonal availability impact snake resource use (Halstead et al., 2008; Nowak et al., 2008), and therefore both intraspecific and

interspecific competition (Luiselli et al., 2002). Niche overlap indices from our study site suggest that the two rattlesnake species potentially partition trophic resources by both prey type (0.28–0.31) and prey size (0.61–0.67). Although these index values were much lower than those for macrohabitat use, suggesting a greater level of possible partitioning, the relationship between macrohabitat use and prey consumption warrants careful consideration. Could the snakes be opportunistically feeding on prey items that differ in availability among the habitats used by the snakes?

Most rattlesnakes, like many (but not all) viperids, are opportunistic predators. *Crotalus ruber* and *C. o. helleri* are no exceptions. Although *C. ruber* relies heavily on rodents at all life stages (Dugan and Hayes, in review), and *C. o. helleri* prefers lizards when young and shifts to rodents as adults (Mackessy, 1988; LaBonte, 2008), both species consume a diversity of prey items within these categories. Indeed, *C. o. helleri* consumed virtually every rodent genera found at our study site (LSA Associates, Inc., 2005). Differences in prey items consumed by the two snake species corresponded largely to prey availability in the different habitats used by the snakes. *Crotalus ruber*, for example, consumed large numbers of wood rats (*Neotoma* spp.), which occur primarily in *C. ruber*'s preferred habitat of cactus and CSS. *Crotalus o. helleri*, in contrast, preyed more often on pocket mice (*Chaetodipus* spp.) and California ground squirrels (*Otospermophilus beecheyi*), which occur primarily in *C. o. helleri*'s preferred grassland habitat. Both rattlesnake species consumed similar numbers of cottontail rabbits (*Sylvilagus* spp.) and deer mice (*Peromyscus* spp.), which occupy a broad range of habitats. Prey size disparity between the rattlesnake species could also result from habitat bias in prey availability (e.g., *C. o. helleri* feeding more on the small grassland rodents),

though body size differences may also contribute, with *C. o. helleri* averaging smaller in size and represented in our sample by more food items procured from neonates. As gape-limited predators (Arnold, 1997; Glaudas et al., 2008; Rodriguez-Robles et al., 1999; Shine, 1991), snakes are constrained by body size in the food items they consume. Thus, we conclude that differential use of macrohabitat could result in reduced overlap, but not necessarily partitioning, of trophic resources. Our findings underscore the difficulty in interpreting niche separation when two or more niche axes covary.

It seems legitimate to contemplate whether innate habitat preferences lead to diet differentiation, or whether innate food preferences lead to habitat differentiation. Niche separation could have an ontogenetic component, with food differing between the younger snakes of the two species, and macrohabitat differing between older snakes. Whereas *C. o. helleri* neonates feed largely on lizard prey (Mackessy, 1988) and preferentially attend to lizard-derived odors in the environment (LaBonte, 2008), *C. ruber* neonates feed largely on rodent prey (Dugan and Hayes, in review). However, all of the *C. o. helleri* neonates at our study site were found with rodent remains, which suggests that an ontogenetic shift in niche separation is unlikely at our study site. Behavioral choice experiments (similar to Bevelander et al., 2006, and Theodoratus and Chiszar, 2000) would be informative for elucidating whether niche separation has an ontogenetic component.

Niche Overlap

To determine whether niche overlap values were significantly less than expected by chance, we subjected them to null models and Monte Carlo simulations. The only evidence for niche partitioning between the two snake species was in prey size, for which

observed index values were significantly less than expected in the null model pseudo-communities. Again, these differences could relate to habitat-specific prey distribution among the different macrohabitats potentially partitioned by the snakes. Index values for temperature were also greater than expected, suggesting that abiotic constraints impose similarity in thermal niche use by the two species. These unexpected results suggest that niche separation between these two rattlesnake taxa has probably resulted largely from non-competitive mechanisms. If niche partitioning exists, we believe it occurs subtly along more than one niche axis, but probably more so via differential habitat use than other axes. If the rattlesnakes we studied partition habitat, we were unable to show this from using contemporary methodology. These findings, therefore, call into question the generality of habitat partitioning by vipers (Luiselli, 2006a, 2006b; Luiselli et al. 2007), and suggest the need for further study.

Acknowledgments

Research was approved by the Loma Linda University Institutional Animal Care and Use Committee, and was conducted under permits issued to the senior author by the California Department of Fish and Game and California State Parks. We thank Bart Grant and Ken Kietzer of Chino Hills State Park for their assistance in our research. We received significant technical and field support from numerous individuals, including M. Cardwell, A. Figueroa, B. McGurty, C. Rodriguez, and S. Bush. The Loma Linda University Department of Earth and Biological Sciences provided financial support for the studies. This project was approved by the Loma Linda University Institutional Animal Care and Use Committee.

References

- ACKERMANN, M., AND M. DOEBELI. 2004. Evolution of niche width and adaptive diversification. *Evolution* 58:2599–2612.
- ADLER, P. B., J. HILLERISLAMBERS, AND J. M. LEVINE. 2007. A niche for neutrality. *Ecology Letters* 10:95–104.
- AEBISCHER, N. J., P. A. ROBERTSON, AND R. E. KENWARD. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313–1325.
- ALBRECHT, M. AND N. J. GOTELLI. 2001. Spatial and temporal niche partitioning in grassland ants. *Oecologia* 126:1343–141.
- ARJO, W. M., D. H. PLETSCHER, AND R. R. REAM. 2002. Dietary overlap between wolves and coyotes in Northwestern Montana. *Journal of Mammalogy* 83:754–766.
- ASHTON, K. G. 1998. Natural history notes: *Pituophis melanoleucus deserticola* (Great Basin gopher snake). Regional heterothermy. *Herpetological Review* 29:170–171.
- AVILA-VILLEGAS, H., M. MARTINS, AND G. ARNAUD. 2007. Feeding ecology of the endemic rattleless rattlesnake, *Crotalus catalinensis*, of Santa Catalina Island, Gulf of California, Mexico. *Copeia* 2007:80–84.
- BEAMAN, K. R., AND E. A. DUGAN. 2006. *Crotalus ruber* (Red Diamond Rattlesnake). *Catalogue of American Amphibians and Reptiles* 840:1–17.
- BEAUPRE, S. J. 2008. Annual variation in time-energy allocation by timber rattlesnakes (*Crotalus horridus*) in relation to food acquisition. Pp. 111–122. *In* W. K. Hayes, K. R. Beaman, M. D. Cardwell, and S. P. Bush (Eds.), *The Biology of Rattlesnakes*. Loma Linda University Press, Loma Linda, California, USA.
- BECK, D. 1995. Ecology and energetics of three sympatric rattlesnake species in the Sonoran Desert. *Journal of Herpetology* 29:211–223.
- BEVELANDER, G., T. L. SMITH, AND K. V. KARDONG. 2006. Microhabitat and prey odor selection in the foraging pygmy rattlesnake. *Herpetologica* 62:47–55.
- BROWN, T. K., J. M. LEMM, MONTAGNE, J-M, AND A. C. ALBERTS. 2008. Spatial ecology, habitat use, and survivorship of resident and translocated red diamond rattlesnakes (*Crotalus ruber*). Pp. 377–394. *In* W. K. Hayes, K. R. Beaman, M. D. Cardwell, and S. P. Bush (Eds.), *The Biology of Rattlesnakes*. Loma Linda University Press, Loma Linda, California, USA.

- CADOTTE, M. W. 2007. Concurrent niche and neutral processes in the competition-colonization model of species coexistence. *Proceedings of the Royal Society B* 247:2739–2744.
- CALENGE, C. 2006 The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modeling*. 197:516–519.
- CAMPBELL, J. A., AND W. W. LAMAR. 2004. The venomous reptiles of the Western hemisphere. 2 volumes. Cornell University Press, Ithaca, New York, USA.
- CHARLAND, B. M., AND P. T. GREGORY. 1990. The influence of female reproductive status on thermoregulation in a viviparous snake, *Crotalus viridis*. *Copeia* 1990:1089–1098.
- CHESSON, P. 2000. Mechanism of maintenance of species diversity. *Annual Review of the Ecology and Systematics* 31:343–366.
- COBB, V. A., J. J. GREEN, T. WORRALL, J. PRUETT, AND B. GLORIOSO. 2005. Initial den location behavior in a litter of neonate *Crotalus horridus* (timber rattlesnake). *Southeastern Naturalist* 4:723–730.
- COHEN, J. 1988. *Statistical power analysis for the behavioral sciences*. 2nd edition. Erlbaum, Hillsdale, New Jersey, USA.
- CONNELL, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35:1313–138.
- CONOVER, W. J. 1999. *Practical Nonparametric Statistics*. 3rd edn. John Wiley and Sons, Inc., New York, New York, USA.
- DESBIEZ, A. L. J., S. A. SANTOS, A. KEUROGHLIAN, AND R. E. BODMER. Niche partitioning among white-lipped peccaries (*Tayassu pecari*), collared peccaries (*Pecari tajacu*), and feral pigs (*Sus scrofa*). *Journal of Mammalogy* 90:119–128.
- DORCAS, M. E., AND C. R. PETERSON. 1997. Head-body temperature differences in free-ranging rubber boas. *Journal of Herpetology* 31:87–93.
- DORCAS, M. E., AND A. W. ROARK. 2000. Regional body temperature variation in corn snakes measured using temperature-sensitive passive integrated transponders. *Journal of Herpetology* 34:481–485.
- DUGAN, E. A., A. FIGUEROA, AND W. K. HAYES. 2008. Home range size, movements, and mating phenology of sympatric red diamond (*Crotalus ruber*) and southern Pacific (*C. oreganus helleri*) rattlesnakes in southern California. Pp. 353–364. *In* W. K. Hayes, K. R. Beaman, M. D. Cardwell, and S. P. Bush (Eds.), *The Biology of Rattlesnakes*. Loma Linda University Press, Loma Linda, California, USA.

- EDGEHOUSE, M. J. 2008. Garter snake (*Thamnophis*) natural history: Food habits and interspecific aggression. Ph.D. Dissertation, Utah State University, Logan, Utah.
- FEINSINGER, P., E. E. SPEARS, AND R. W. POOLE. 1981. A simple measure of niche overlap. *Ecology* 62:27–32.
- FELLERS, G. M., AND P. M. KLEEMAN. 2007. California red-legged frog (*Rana draytonii*) movement and habitat use: Implications for conservation. *Journal of Herpetology* 41:276–286.
- FUKADA, H. 1992. Snake Life History in Kyoto. Impact Shuppankai, Kyoto, Japan.
- GAUSE, G. F. 1934. *The Struggle for Existence*. William and Wilkins, Baltimore, Maryland, USA.
- GARDNER-SANTANA, L. C., AND S. J. BEAUPRE. 2009. Timber rattlesnakes (*Crotalus horridus*) exhibit elevated and less variable body temperatures during pregnancy. *Copeia* 2009:363–368.
- GERSTELL, A. T., AND J. C. BEDNARZ. 1999. Competition and patterns of resources use by two sympatric raptors. *Condor* 101:557–565.
- GILLIHAN, S. W., AND K. R. FORESMAN. 2004. *Sorex vagrans*. *Mammalian Species* 744:1–5.
- GLAUDAS, X., T. JEZKOVA, AND J. A. RODRIGUES-ROBLES. 2008. Feeding ecology of the Great Basin rattlesnake (*Crotalus oreganus lutosus*, Viperidae). *Canadian Journal of Zoology* 86:1–12.
- GOLDBERG, S. R. 1999. Reproduction in the red diamond rattlesnake in California. *California Fish and Game* 85:177–180.
- GOODYEAR, S. E., AND E. R. PIANKA. 2008. Sympatric ecology of five species of fossorial snakes (Elapidae) in western Australia. *Journal of Herpetology* 42:279–285
- GORAN, N., C. ANDREN, AND Y. IOANNIDIS. 1999. Ecology and conservation of the Milos viper, *Macrovipera schweizeri* (Werner, 1935). *Amphibia-Reptilia* 20:355–375.
- GOTELLI, N.J., AND G.L. ENTSMINGER. 2001. EcoSim: Null models software for ecology. Version 7.71. Acquired Intelligence Inc. and Kesey-Bear. <http://homepages.together.net/~gentsmin/ecosim.htm>
- GOTELLI, N.J., AND G.R. GRAVES. 1996. *Null models in ecology*. Smithsonian Institution Press.

- GREENBERG, D. B. 2002. The ecology of movement and site selection in desert rattlesnakes (*Crotalus mitchellii* and *Crotalus ruber*) of the southwestern United States. Ph.D. Dissertation, University of California, Santa Barbara, California, USA.
- GRISMER, L. L. 2002. Amphibians and Reptiles of Baja California including its Pacific Islands and the Islands in the Sea of Cortes. University of California Press, Berkeley, California, USA.
- HALSTEAD, B. J., H. R. MUSHINSKY, AND E. D. MCCOY. 2008. Sympatric *Masticophis flagellum* and *Coluber constrictor* select vertebrate prey at different levels of taxonomy. *Copeia* 2008:897–908.
- HARDY, D. L., AND H. W. GREENE. 1999. Surgery on rattlesnakes in the field for implantation of transmitters. *Sonoran Herpetologist* 12:26–28.
- HARDY, D. L., H. W. GREENE, AND C. S. RAU. 2001. Anesthesia and surgical techniques for radio-telemetry in rattlesnakes. SEASERG & SARC Productions. Portal, AZ, USA.
- HARTMANN, P. A., AND A. V. MARQUES. 2005. Diet and habitat use of two sympatric species of *Philodryas* (Colubridae), in south Brazil. *Amphibia-Reptilia* 26:25–31.
- HARVEY, D. S., AND P. J. WEATHERHEAD. 2010. Habitat selection as the mechanism for thermoregulation in a northern population of massasauga rattlesnakes (*Sistrurus catenatus*). *Ecoscience* 17:411–419.
- HESKE, E. J., R. S. OSTFELD, AND W. Z. LIDICKER, JR. 1984. Competitive interactions between *Microtus californicus* and *Reithrodontomys megalotis* during two peaks of *Microtus* abundance. *Journal of Mammalogy* 65:271–280.
- JAMESON, E. W., JR., AND H. J. PEETERS. 1988. Mammals of California. University of California Press, Berkeley, California, USA.
- JENNINGS, M. R., AND M. P. HAYES. 2004. Amphibian and reptile species of special concern in California. California Department of Fish and Game, Rancho Cordova, California, USA.
- KLAUBER, L. M. 1972. Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind. 2nd ed. 2 vol. University of California Press, Berkeley, California, USA.
- KOZLOWSKI, A. J., E. M. GESE, AND W. M. ARJO. 2008. Niche overlap and resource partitioning between sympatric kit foxes and coyotes in the Great Basin desert of western Utah. *American Midland Naturalist* 160:191–208.

- LABONTE, J. P. 2008. Ontogeny of prey preference in the southern Pacific rattlesnake, *Crotalus oreganus helleri*. Pp. 169–174. In W. K. Hayes, K. R. Beaman, M. D. Cardwell, and S. P. Bush (Eds.), *The Biology of Rattlesnakes*. Loma Linda University Press, Loma Linda, California, USA.
- LAAKKONEN, J. 2003. Effect of arboreal activity on species composition and abundance estimates of rodents in a chaparral habitat in southern California. *American Midland Naturalist* 150:348–351.
- LAURENT, E. J., AND B. A. KINGSBURY. 2003. Habitat separation among three species of water snakes in northwestern Kentucky. *Journal of Herpetology* 37:229–235.
- LEHSTEN, V., AND P. HARMAND. 2006. Null models for species co-occurrence patterns: assessing bias and minimum iteration number for the sequential swap. *Ecography* 29:786–792.
- LILLYWHITE, H. B., C. M. SHEEHY, III, AND F. ZAIDEN, III. 2008. Pitviper scavenging at the intertidal zone: An evolutionary scenario for invasion of the sea. *Bioscience* 58:947–955.
- LIN, W-C., Y-H., HSIN, AND K-Y. LUE. 2007. Diurnal retreat site selection by the arboreal Chinese green tree viper (*Trimeresurus s. stejnegeri*) as influenced by body temperature. *Zoological Studies* 46:216–226.
- LSA ASSOCIATES, INC. 2005. 2005 rodent survey of the Puente Hills Landfill Native Habitat Preservation Authority Lands. LSA Associates, Inc., Irvine, California, USA.
- LUISELLI, L. 2003. Do snakes exhibit shifts in feeding ecology associated with the presence or absence of potential competitors? A case study from tropical Africa. *Canadian Journal of Zoology* 81:228–236.
- LUISELLI, L. 2006a. Resource partitioning and interspecific competition in snakes: The search for general geographical and guild patterns. *Oikos* 114:193–211.
- LUISELLI, L. 2006b. Food niche overlap between sympatric potential competitors increases with habitat alteration at different trophic levels in rain-forest reptiles (omnivorous tortoises and carnivorous vipers). *Journal of Tropical Ecology* 22:695–704.
- LUISELLI, L., AND C. G. AKANI. 2003. Diet of sympatric gaboon vipers (*Bitis gabonica*) and nose-horned vipers (*Bitis nasicornis*) in southern Nigeria. *African Journal of Ecology* 52:101–106.
- LUISELLI, L., F. M. ANGELICI, AND G. C. AKANI. 2002. Comparative feeding strategies and dietary plasticity of the sympatric cobras *Naja melanoleuca* and *Naja*

- nigricollis* in three diverging Afrotropical habitats. Canadian Journal of Zoology 80:55–63.
- LUISELLI, L., E. FILIPPI, AND E. DI LENA. 2007. Ecological relationships between sympatric *Vipera aspis* and *Vipera ursinii* in high-altitude habitats of Central Italy. Journal of Herpetology 41:378–384.
- MACARTNEY, J. M. 1989. Diet of the northern Pacific rattlesnake, *Crotalus viridis oreganus*, in British Columbia. Herpetologica 45:299–304.
- MACKESSEY, S. P. 1988. Venom ontogeny in the Pacific rattlesnakes *Crotalus viridis helleri* and *C. v. oreganus*. Copeia 1988:92–101.
- MARTINS, M., G. ARNAUD, AND R. MURILLO-QUERO. 2008. Exploring hypotheses about the loss of the rattle in rattlesnakes: How arboreal is the Isla Santa Catalina rattleless rattlesnake, *Crotalus catalinensis*. South American Journal of Herpetology 3:162–167.
- M'CLOSKEY, R. T. 1972. Temporal changes in populations and species diversity in a California rodent community. Journal of Mammalogy 53:657–676.
- MENDELSON, J. R., III, AND W. B. JENNINGS. 1992. Shifts in the relative abundance of snakes in a desert grassland. Journal of Herpetology 26:38–45.
- MERTLER, C. A., AND R. A. VANNATTA. 2004. Advanced and Multivariate Statistical Methods: Practical Application and Interpretation. 3rd Edition. Pyczak Publishing, Los Angeles, California, USA.
- MESERVE, P. L. 1974. Temporary occupancy of a coastal sage scrub community but a seasonal immigrant, the California mouse (*Peromyscus californicus*). Journal of Mammalogy 55:836–840.
- MESERVE, P. L. 1976. Habitat and resource utilization by rodents of a California coastal sage scrub community. Journal of Animal Ecology 45:647–666.
- MONNEY, J.-C. 1996. Biologie comparée de *Vipera aspis* L. et de *Vipera berus* L. (Reptilia, Ophidia, Viperidae) dans une station des Préalpes Bernoises. Ph.D. Dissertation, University of Neuchâtel, Neuchâtel, Switzerland.
- MURPHY, R. W., J. FU, A. LATHROP, J. V. FELTHAM, AND V. KOVAC. 2002. Phylogeny of the rattlesnakes (*Crotalus* and *Sistrurus*) inferred from sequences of five mitochondrial DNA genes. Pp. 69–92. In G. W. Schuett, M. Höggren, M. E. Douglas, and H. W. Greene (Eds). Biology of the Vipers. Eagle Mountain Publishing, LC, Eagle Mountain, Utah, USA.

- MUSHINSKY, H. R., J. J. HEBRARD, AND M. G. WALLEY. 1980. The role of temperature on the behavior and ecological associations of sympatric water snakes. *Copeia* 1980:744–754.
- NAKAGAWA, S. 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. *Behavioral Ecology* 15:1044–1045.
- NOSS, R. F., AND R. L. PETERS. 1995. *Endangered Ecosystems. A Status Report on America's Vanishing Habitat and Wildlife*. Defenders of Wildlife, Washington, D.C., USA.
- NOWAK, E. M., T. C. THEIMER, AND G. W. SCHUETT. 2008. Functional and numerical responses of predators: Where do vipers fit in the traditional paradigms? *Biological Reviews* 83:601–620.
- PAVLIK, S. 2007. Arboreal behavior in the tiger rattlesnake (*Crotalus tigris*). *Sonoran Herpetologist* 20:56.
- PFENNIG, D. W., A. M. RICE, AND R. A. MARTIN. 2006. Ecological opportunity and plasticity interaction to promote character displacement and species coexistence. *Ecology* 87:769–779.
- PIANKA, E. R. 1975. Niche relations of desert lizards. Pp. 292–314. *In* M. L. Cody and J. M. Diamond (Eds.), *Ecology and Evolution of Communities*. Harvard University Press, Cambridge, Massachusetts, USA.
- PIANKA, E. R. 1981. Competition and niche theory. Pp. 167–196. *In* R. May (Ed.), *Theoretical Ecology. Principles and Applications*. Blackwell, Oxford, UK.
- POUGH, H. 1966. Ecological relationships of rattlesnakes in southeast Arizona with notes on other species. *Copeia* 1966:676–683.
- REICHENBACH, N. G., AND G. H. DALRYMPLE. 1980. On the criteria and evidence for interspecific competition in snakes. *Journal of Herpetology* 14:409–412.
- REINERT, H. K. 1984. Habitat separation between sympatric snake populations. *Ecology* 65:478–486.
- REINERT, H. K. 1993. Habitat selection in snakes. Pp. 201–240. *In* R. A. Seigel and J. T. Collins (Eds.), *Snakes: Ecology and Behavior*. McGraw-Hill, Inc., New York, New York, USA.
- REINERT, H. K., AND D. CUNDALL. 1982. An improved surgical implantation method for radio-tracking snakes. *Copeia* 1982:702–705.

- REYNOLDS, R. P., AND N. J. SCOTT, JR. 1982. Use of a mammalian resource by a Chihuahuan snake community. Pp. 99–118. *In* N. J. Scott, Jr. (Ed.), *Herpetological Communities*. U.S. Department of Interior, Fish and Wildlife Service, Wildlife Research Report 13.
- RICHARDSON, M. L., P. J. WEATHERHEAD, AND J. D. BRAWN. 2006. Habitat use and activity of prairie kingsnakes (*Lampropeltis calligaster calligaster*) in Illinois. *Journal of Herpetology* 40:423–428.
- RODRIGUEZ-ROBLES, J. A., C. J. BELL, AND H. W. GREENE. 1999. Gape size and evolution of diet in snakes: Feeding ecology of erycine boas. *Journal of Zoology* 248:49–58.
- RUDOLPH, D. C., R. R. SCHAEFER, D. SAENZ, AND R. N. CONNER. 2004. Arboreal behavior in the timber rattlesnake, *Crotalus horridus*, in eastern Texas. *Texas Journal of Science* 54:395–404.
- SAJDAK, R. A., AND A. W. BARTZ. 2004. *Crotalus horridus* (timber rattlesnake). Arboreality, diet. *Herpetological Review* 31:60–61.
- SAINT GIRONS, H. 1975. Coexistence de *Vipera aspis* et de *Vipera berus* en Loire Atlantique: Un problème de compétition interspécifique. *Revue d'Ecologie (La Terre et la Vie)* 29:590–613.
- SAINT GIRONS, H. 1978. Thermorégulation comparé de vipères d'Europe. Etude biotéléométrique. *Revue d'Ecologie (La Terre et la Vie)* 32:417–439.
- SANTOS DAYRELL, J., H. C. COSTA, R. N. FEIO, AND L. O. DRUMMOND. 2010. *Crotalus durissus* (South American rattlesnake) arboreal habitat use. *Herpetological Review* 41:89–90.
- SAMPSON, G. T. 1985. The flora of Chino Hills State Park. M.A. Thesis, California State University, Fullerton, USA.
- SCHETTINO, L. R., J. B. LOSOS, P. E. HERTZ, K. DE QUEIROZ, A. R. CHAMIZO, M. LEAL, AND V. R. GONZALEZ. 2010. The anoles of Soroa: Aspects of their ecological relationships. *Breviora* 520:1–22.
- SCHLUTER, D. 1995. *The Ecology of Adaptive Radiation*. Oxford University Press, Oxford, UK.
- SCHOENER, T. W. 1974. Resource partitioning in ecological communities. *Science* 185:27–39.
- SHEPARD, D. B., C. A. PHILLIPS, M. J. DRESLIK, AND B. C. JELLEN. 2004. Prey preference and diet of neonate eastern massasaugas (*Sistrurus c. catenatus*). *American Midland Naturalist* 152:360–368.

- SHINE, R. 1991. Why do larger snakes eat larger prey items? *Functional Ecology* 5:493–502.
- SHINE, R., AND X. BONNET. 2000. Snakes: A new "model organism" in ecological research? *Trends in Ecology and Evolution* 15:221–222.
- SPSS. 2004. SPSS for Windows, version 13.0. SPSS, Inc., Chicago, Illinois, USA.
- STEBBINS, R. C. 1985. *A Field Guide to Western Reptiles and Amphibians*. 2nd edn. Houghton Mifflin Company, Boston, Massachusetts, USA.
- STEEN, D. A., L. L. SMITH, L. M. CONNER, J. C. BROCK, AND S. K. HOSS. 2007. Habitat use of sympatric rattlesnake species within the Gulf Coastal Plain. *Journal of Wildlife Management* 71:759–764.
- TANAKA, K., AND H. OTA. 2002. Natural history of two colubrid snakes, *Elaphe quadrivirgata* and *Rhabdophis tigrinus*, on Yakushima Island, southwestern Japan. *Amphibia Reptilia* 23:323–331.
- TAYLOR, E. N., AND D. F. DENARDO. 2008. Proximate determinants of sexual size dimorphism in the western diamond-backed rattlesnake (*Crotalus atrox*). Pp. 91–100. *In* W. K. Hayes, K. R. Beaman, M. D. Cardwell, and S. P. Bush (Eds.), *The Biology of Rattlesnakes*. Loma Linda University Press, Loma Linda, California, USA.
- THEODORATUS, D. H., AND D. CHISZAR. 2000. Habitat selection and prey odor in the foraging behavior of western rattlesnakes (*Crotalus viridis*). *Behaviour* 137:119–135.
- THORNTON, D. H., M. E. SUNQUIST, AND M. B. MAIN. 2004. Ecological separation within newly sympatric populations of coyotes and bobcats in south-central Florida. *Journal of Mammalogy* 85:973–982.
- TOFT, C. A. 1985. Resource partitioning in amphibians and reptiles. *Copeia* 1985:1–21.
- TOWNSEND, C, M. BEGON, AND J. L. HARPER. 2008. *Essentials of Ecology*. 3rd edn. Blackwell Publishing, Oxford, UK.
- VERGNON, R., N. K. DULVY, AND R. P. FRECKLETON. 2009. Niches versus neutrality: Uncovering the drivers of diversity in a species-rich community. *Ecology Letters* 12:1079–1090.
- VOLTERRA, V. 1926. Fluctuations in the abundance of a species considered mathematically. *Nature* 118:196–218.

WALDRON, J. L., S. H. BENNETT, S. M. WELCH, M. E. DORCAS, J. D. LANHAM, AND W. KALINOWSKY. 2006. Habitat specificity and home-range size as attributes of species vulnerability to extinction: A case study using sympatric rattlesnakes. *Animal Conservation* 9:414–420.

WALTER, G. H. 1991. What is resource partitioning? *Journal of Theoretical Biology* 150:137–143.

WASKO, D. K., AND M. SASA. 2010. Habitat selection of the terciopelo (Serpentes: Viperidae: *Bothrops asper*) in a lowland rainforest in Costa Rica. *Herpetologica* 66:148–158.

WINEMILLER, K. O., AND E. R. PIANKA. 1990. Organization in natural assemblages of desert lizards and tropical fishes. *Ecological Monographs* 60:27–55.

ZAR, J. H. 1996. *Biostatistical Analysis*, 3rd ed. Prentice Hall, Englewood Cliffs, New Jersey, USA.

CHAPTER FOUR
DIET AND FEEDING ECOLOGY OF THE RED DIAMOND
RATTLESNAKE, *CROTALUS RUBER* (SERPENTES: VIPERIDAE)

ERIC A. DUGAN^{1,2} AND WILLIAM K. HAYES¹

¹*Department of Earth and Biological Sciences, Loma Linda University,
Loma Linda, CA 92350 USA*

A revised version of this chapter has been published with the following citation:

DUGAN, E. A. AND W. K. HAYES. 2012. Diet and Feeding Ecology of the Red Diamond Rattlesnake, *Crotalus ruber* (Serpentes: Viperidae) *Herpetologica* 68(2): 203–217.

Abstract

Studies of diet are central to our understanding of organismal biology. We describe the diet of the red diamond rattlesnake (*Crotalus ruber*) using data collected from museum specimens, live specimens from a field study, road kills, opportunistic behavioral observations, and existing literature. Dietary samples were collected from across the species' range, including southern California (USA) and Baja Norte and Baja Sur (Mexico). Examination of 265 individuals resulted in 227 prey items recorded from 219 snakes. The diet of *C. ruber* consisted largely of mammals (91.6%), but also included lizards (7.5%) and birds (0.9%). No ontogenetic shift in prey type was evident, with mammals consumed by all snake size classes. However, adults fed on larger prey than juveniles. Sexual dimorphism existed in snake length, with adult males averaging longer than adult females. Juvenile males consumed larger prey than females, but no sexual differences in prey mass existed for adults when controlling for snake body length. Snakes from coastal populations averaged longer in body length than snakes from desert populations. Coastal snakes consumed a higher proportion of rodents, and prey of larger body mass when controlling for snake length, than snakes from desert populations. The presence of prey was independent of snake collection month, suggesting year-round feeding, as supported by observations of occasional feeding by radio-tracked snakes in California. Although *C. ruber* may scavenge food opportunistically, behavioral observations suggest it relies heavily on ambushing mammal prey.

Introduction

Studies of diet embody organismal biology, offering insights into the broader ecology of a species, including distribution patterns (Greene, 1993) and evolutionary divergence (Darwin, 1859; Creer et al., 2002; Zelanis et al., 2008). Considered exceptional model systems for studies of diet (Shine and Bonnet, 2000), snakes provide opportunities to examine organisms with unique adaptations for feeding and foraging (Greene, 1997). As such, diets are considered driving forces of snake evolution (Greene, 1983), and have broad implications for habitat use (Lillywhite et al., 2008; Shine and Li-Xin, 2002), movements (Clark, 2006), interspecific competition (Luiselli, 2006), and the development of conservation strategies for predators and/or prey (Holycross et al., 2002*b*; Lewis et al., 2010).

Ontogenetic variation in diet is well documented among vipers (e.g., Hartmann et al., 2005; Jadin, 2007; Martins et al., 2001; Zelanis et al., 2008), and rattlesnakes in particular (e.g., Glaudas, et al., 2008; Holycross and Mackessy, 2002; LaBonte, 2008; Mackessy, 1988; Taylor, 2001). As gape-limited predators, snakes utilize prey bases determined to a great extent by prey diameter (Arnold, 1997; Glaudas et al., 2008; Rodriguez-Robles et al., 1999; Shine, 1991*a*). Most species shift from smaller ectothermic prey as juveniles to larger endothermic prey as adults. However, not all rattlesnakes demonstrate this transition (da Graça Salomão et al., 1995). Understanding ontogenetic shifts in diet helps explain predator-prey relationships (Diller and Wallace, 1996), age-dependent habitat use and foraging tactics (Figueroa et al., 2008; LaBonte et al., 2008), optimal foraging strategies (Costa et al., 2008), and functional constraints on prey acquisition, venom use, and venom composition (Hayes, 2008; Herbert and Hayes, 2008; Mackessy, 1988; Mackessy et al., 2003).

Most snake species exhibit sexual dimorphism in body size, with females larger than males (Fitch, 1981). However, most rattlesnakes, particularly the larger species, exhibit male-larger sexual size dimorphism (Taylor and DeNardo, 2008). Sexual head size dimorphism has also been documented in rattlesnakes (Glaudas et al., 2008; Klauber, 1972), and may be associated with sexual differences in diet (Glaudas et al., 2008; Vincent et al., 2004), though no such differences have been reported for rattlesnakes.

Widespread snake species often exhibit geographic variation in diet (Creer et al., 2003, Hartmann et al., 2005). Several rattlesnakes demonstrate this variation (Clark, 2002; Glaudas et al., 2008; Holycross and Mackessy, 2002), whereas others utilize a similar diet throughout their range (Holycross et al., 2002a; Spencer, 2003).

Understanding geographic variation in diet can benefit our knowledge of venom composition (Barlow et al., 2009; Creer et al., 2003; Daltry et al., 1996) and, potentially, trophic morphology (Pleguezuelos et al., 2007; Vincent et al., 2009). Most temperate snakes feed primarily during the warm “active” season. However, thermal constraints may be different for rattlesnakes in warmer climates, permitting occasional winter or even year-round feeding (e.g., Martin and Means, 2000), with concomitant fitness benefits such as more rapid growth and more frequent reproduction (Taylor and DeNardo, 2008).

The red diamond rattlesnake (*Crotalus ruber*) is a large-bodied snake, reaching an adult size of ca. 1200 mm SVL. It ranges from San Bernardino County, California, USA, south to the tip of the Baja Peninsula, Baja California Sur, Mexico. In Mexico, insular populations exist on the Pacific Islands of Cedros and Santa Margarita (Wong, 1997), and

on the Gulf Islands of Angel de la Guarda, Dazante, Monserrate, Pond, San Jose, and San Marcos (Grismer, 2002).

The species occupies a wide range of habitats, including desert slopes, rocky canyons, and coastal foothills (Grismer, 2002). Within the United States, *C. ruber* inhabits a relatively restricted range (Beaman and Dugan, 2006). Coastal populations in California are under immense pressure from urbanization and development (Brown et al., 2008; Halama et al., 2008). According to some estimates, the distribution of coastal sage-scrub ecosystems in California has declined by as much as 90% from historical levels (Noss and Peters, 1995), prompting the state to list *C. ruber* as a Species of Special Concern (Jennings and Hayes, 1994).

As a large-bodied rattlesnake that occupies a moderately large range and inhabits a wide array of habitats, *C. ruber* represents an excellent species to examine potential ontogenetic and geographic variation in diet. Herein, we describe the diet of this understudied species.

Materials and Methods

Sources of Prey Items

Using an integrated approach (Saviozzi and Zuffi, 1997), we obtained dietary data from museum specimens, live specimens from a field study, roadkills, opportunistic behavioral observations, and existing literature.

We examined 145 specimens of *C. ruber* from the following institutional collections: Los Angeles County Museum of Natural History (LACM, $n = 110$), San Diego Natural History Museum (SDNHM, $n = 29$), and Anza Borrego Desert State Park (ABDSP, $n = 6$; Appendix 4-1). Institutional codes follow Leviton et al. (1985). For

preserved specimens, a mid-ventral incision was made to determine presence/absence of food items in stomach contents and fecal matter. Fragile specimens, those maintained in captivity for extensive periods, and those whose collection data indicated compromised diets and/or prey items (e.g., domesticated mice, *Mus musculus*, presumably from captive feeding) were omitted. For each snake, we recorded SVL, sex, collection locality, and number and identity of prey items. Snake mass was not recorded given the inaccuracy of weight measurements associated with preserved specimens.

We collected 22 fecal samples opportunistically from live snakes in Chino Hills State Park, California, USA, as part of a larger radio-telemetry study of *C. ruber* biology from 2003–2009 (Dugan et al., 2008). Snakes containing food boli were not palpated or forced to regurgitate food items (Macartney, 1989). However, snakes occasionally defecated while being held for processing and/or radio-transmitter implantation.

We also located 70 published records (Grismer, 2002; Klauber, 1972; Patten and Banta, 1980; Tevis, 1943), which often consisted of only the prey species, and therefore lacked additional data. Another 22 records were represented by direct observations of live or road-killed animals, some shared by trusted colleagues.

Our combined sample included *C. ruber* collected in Imperial County (USA, $n = 1$), Riverside County (USA, $n = 66$), San Bernardino County (USA, $n = 23$), San Diego County (USA, $n = 75$), Orange County (USA, $n = 10$), Baja Norte, Mexico (MX, $n = 22$), Baja Sur, Mexico (MX, $n = 10$), Baja region in general (MX, $n = 28$), and unknown location ($n = 36$).

Identification of Prey Items

Prey items and stomach, gut, and fecal contents were stored individually in sealed glass vials containing 70% ethanol. Prey items were classified as lizards, birds, or mammals. To identify mammal prey to genus or species, dorsal guard hairs were cut in half at the widest point and soaked in xylene 24 hr to allow maximum penetration of the medulla (Moore et al., 1974). Resulting hairs were mounted on glass slides using TBS Shur/Mount toluene-based liquid mounting media (Triangle Biomedical Sciences, Inc., Durham, NC, USA), and allowed to set for a minimum of 4 hr using a glass cover slip. Samples were identified to the lowest possible taxonomic level by comparison to known dorsal guard hair patterns observed under a light microscope (Moore et al., 1974). On occasion, bone, teeth, nails, and skulls were recovered in addition to hair. When possible, multiple diagnostics (e.g., teeth and dorsal guard hair pattern) were used to identify prey items, drawing from the mammal collection at Loma Linda University. Lizards were identified using diagnostic scale characteristics of sympatric species (Stebbins, 1985). The single intact bird was identified by a photograph of the remains (K. R. Beaman and K. L. Garrett, personal communication). We often used the known distribution of prey species (i.e., allopatric ranges) to reach species-level identification (Jameson and Peeters, 1988).

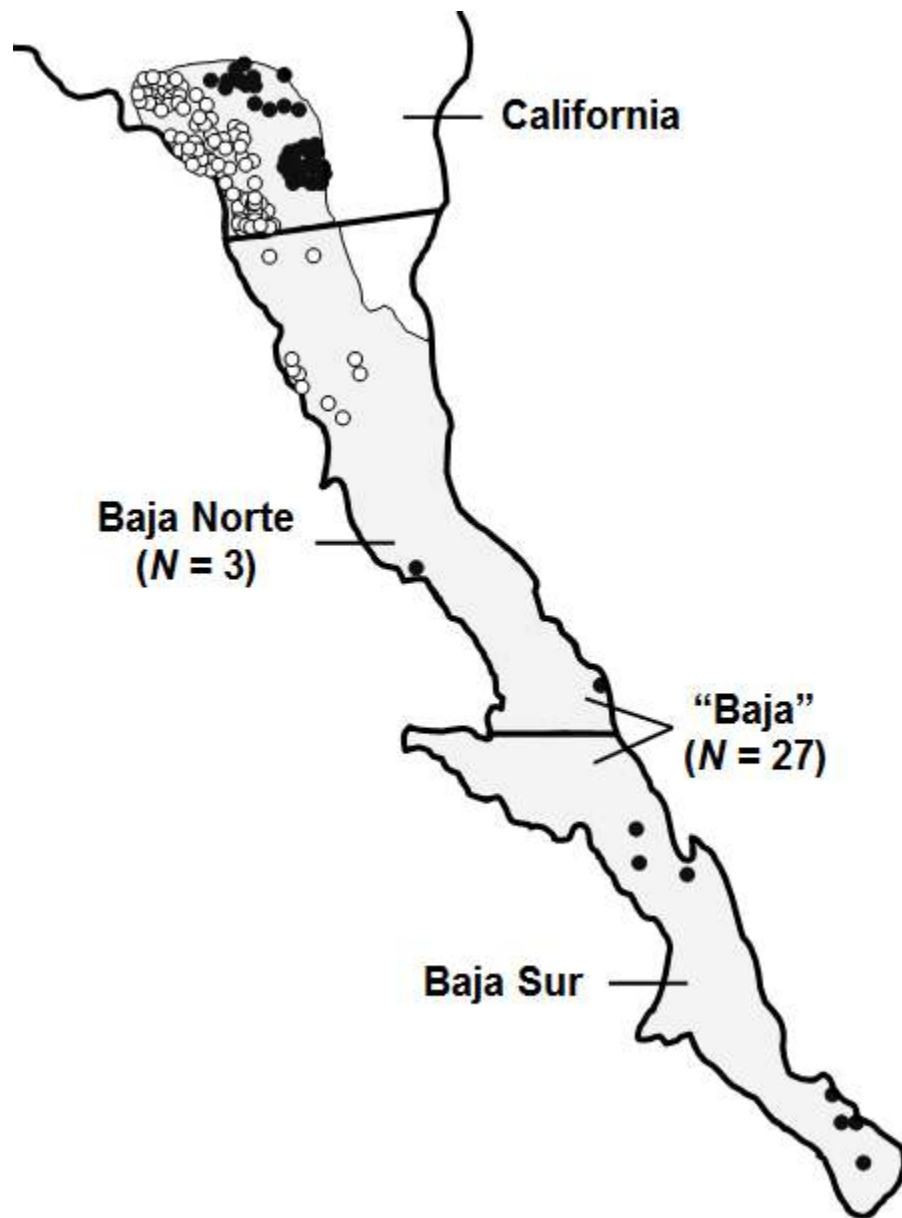


FIG. 4-1.—Locations of red diamond rattlesnake (*Crotalus ruber*) specimens yielding prey items from coastal (unfilled circles) and desert (filled circles) populations in California (USA) and the two states of Baja California (Mexico). Numbers of specimens having only regional locality data are indicated within parentheses; habitat types were not assigned to these.

Sources of Dietary Variation

To assess ontogenetic variation and possible shifts in diet, snakes were classified as juveniles (≤ 600 mm SVL) or adults (>600 mm SVL) based on minimum reproductive size (Goldberg, 1999), although the sexes attain sexual maturity at slightly different sizes. We also used absolute snake length. Because most prey items were of unknown size, we assigned to all items an average adult mass obtained from the literature for each reptile (*Aspidoscelis* and *Sceloporus*: Bonine and Garland, 1999; *Ctenosaura*: Carothers, 1983), bird (Sibley, 2000), and mammal (Jameson and Peeters, 1988) species; many prior studies have used this approach. For these analyses, snakes with multiple prey items of different species were excluded to avoid pseudoreplication. To assess sexual variation, we determined sex by probing for hemepenes and/or relative tail length. To assess geographic variation, we coded individual snakes into one of two groups: desert or coastal. The desert group contained snakes whose collection localities were characterized by summer-dominated rainfall, and the coastal group included those that originated from a Mediterranean climate of winter-dominated rainfall (c.f. Schoenherr, 1992; Fig. 4-1). To assess temporal variation, we considered month of collection as well as two seasons of activity: active (March–November) and winter (December–February; Dugan et al., 2008).

Analyses

We relied on parametric tests when assumptions were met (Zar, 1996), including the independent-samples *t*-test, Pearson's correlation (*r*), and analysis of covariance (ANCOVA). We also employed non-parametric tests for categorical data (Zar, 1996), including the Chi-square test (χ^2) and Spearman's rank correlation (*r_s*). Following

Nakagawa (2004), we chose not to adjust alpha for multiple tests. We further computed effect sizes, which are independent of sample size (in contrast to statistical significance) and more readily compared among different data sets and different studies. For pairwise comparisons (*t*-tests), we relied on Cohen's *d* using pooled standard deviation (Hojat and Xu, 2004), for which values of ~ 0.5 are generally considered moderate and ≥ 0.8 large (Cohen, 1988). For ANCOVA, we computed partial eta-squared (η^2), with values of ~ 0.06 regarded moderate and ≥ 0.14 large (Cohen, 1988). For tests of proportions (χ^2), we computed Phi (ϕ) for 2×2 and Cramer's *V* for 2×3 contingency tables, with values of ~ 0.3 deemed moderate and ≥ 0.5 large (Cohen, 1988). Finally, we expressed bivariate correlations (Pearson's *r*) as coefficients of determination (r^2), with values of ~ 0.9 considered moderate and ≥ 0.25 large (Cohen, 1988). With the exception of Cohen's *d*, these effect size estimators roughly indicate the approximate proportion of variance explained. The terms "moderate" and "large" are used loosely. Statistical tests were conducted using SPSS 13.0 for Windows (Statistical Package for the Social Sciences, Inc., Chicago, 2004), with alpha = 0.05.

Results

Prey Items

Of the 265 *C. ruber* individuals in the database, 219 (82.6%) snakes yielded 227 prey items that were at least partially identifiable (Table 4-1). Eighty-two (36.1%) prey records were recorded from fecal contents, 61 (26.9%) from stomach contents, 55 (24.2%) from literature sources, and 29 (12.8%) from snakes observed feeding in the field. Seven snakes contained multiple prey items (3.2%); of these, one was observed consuming three prey (all mammals), and six contained two mammals. Identifying

multiple prey was possible from gut contents and feces only if two different species were found, leading to underestimation. Ninety-four of 141 (66.7%) museum specimens contained 100 identifiable prey items, 39 from stomach contents and 61 from gut contents.

The proportion of snakes containing food items varied regionally due to variation in sampling methods: Imperial County, 0% of 1 specimen; Riverside County, 59.1% of 66 specimens; San Bernardino County, 100% of 23 (primarily fecal samples); San Diego County, 92.0% of 75 (primarily selected museum records); Orange County, 60.0% of 10; Baja Norte, 54.5% of 22; Baja Sur, 60.0% of 10; Baja region, 100% of 28 (primarily literature records); and unknown location, 100% of 36 (entirely literature records).

Among the 227 prey items (Table 4-1), we identified remains of 208 (91.6%) mammals, 17 (7.5%) lizards, and two (0.9%) birds. The 114 mammal remains identifiable to genus were widely distributed among 12 genera: *Ammospermophilus* (4.4%); *Chaetodipus* (15.1%); *Dipodomys* (15.1%); *Microtus* (2.5%); *Neotoma* (21.0%); *Onychomys* (5.0%); *Otospermophilus* (8.4%); *Peromyscus* (15.1%); presumably feral *Rattus* (0.8%); *Reithrodontomys* (0.8%); *Spilogale* (0.8%); *Sylvilagus* (10.1%); and *Thomomys* (0.8%). The 12 lizards identifiable to genus comprised three genera, including whiptail lizards (*Aspidoscelis*, 66.7%), an adult *Ctenosaura hemilopha* iguana (8.3%) consumed by a 1155 mm snake from Baja California Sur, and *Sceloporus* (25.0%). Remains of the only identifiable bird (*Pipilo crissalis*) were voluntarily regurgitated from a 915 mm snake collected along the coast.

TABLE 4-1.—Prey consumed by *Crotalus ruber*, including frequency (*n*), proportion of total items, and proportion of identifiable items within classes Aves, Mammalia, and Reptilia. See Methods for literature sources of prey mass.

Prey taxon (adult mass, g)	<i>n</i>	% of total (% of identified)	Source
Aves	2	0.9	
<i>Pipilo crissalis</i> (44 g)	1	0.4 (100.0)	This study
Unidentified Bird	1	0.4 (0.0)	Klauber, 1972
Mammalia	208	91.6	
<i>Ammospermophilus leucurus</i> (90 g)	5	2.2 (4.4)	Tevis, 1943; this study
<i>Dipodomys agilis</i> (73 g)	3	1.3 (2.5)	This study
<i>Dipodomys deserti</i> (110 g)	1	0.4 (0.8)	Patten and Banta, 1980
<i>Dipodomys merriami</i> (65 g)	4	1.8 (3.4)	Tevis 1943; this study
<i>Dipodomys</i> spp (85 g)	10	4.4 (8.4)	This study
<i>Microtus californicus</i> (60 g)	3	1.3 (2.5)	This study
<i>Neotoma fuscipes</i> (275 g)	16	7.0 (13.4)	This study
<i>Neotoma lepida</i> (145 g)	3	1.3 (2.5)	Klauber, 1972; this study
<i>Neotoma</i> spp. (210 g)	6	2.6 (5.0)	This study
<i>Onychomys torridus</i> (23 g)	6	2.6 (5.0)	This study
<i>Chaetodipus californicus</i> (19 g)	1	0.4 (0.8)	This study
<i>Chaetodipus fallux</i> (17 g)	1	0.4 (0.8)	This study
<i>Chaetodipus longimembris</i> (9 g)	1	0.4 (0.8)	This study
<i>Chaetodipus</i> spp. (15 g)	15	6.6 (12.6)	This study
<i>Peromyscus californicus</i> (45 g)	3	1.3 (2.5)	This study
<i>Peromyscus crinitus</i> (15 g)	3	1.3 (2.5)	This study
<i>Peromyscus eremicus</i> (24 g)	3	1.3 (2.5)	This study
<i>Peromyscus</i> spp. (28 g)	9	4.0 (7.6)	This study
<i>Rattus</i> spp. (275 g)	1	0.4 (0.8)	This study
<i>Reithrodontomys megalotis</i> (12 g)	1	0.4 (0.8)	This study
<i>Otospermophilus californicus</i> (475 g)	10	4.4 (8.4)	This study
<i>Spilogale gracilis</i> (750 g)	1	0.4 (0.8)	Klauber, 1972
<i>Sylvilagus audubonii</i> (950 g)	11	4.8 (9.2)	Klauber, 1972; this study
<i>Sylvilagus bachmani</i> (795 g)	1	0.4 (0.8)	
<i>Thomomys bottae</i> (154 g)	1	0.4 (0.8)	This study
Unidentified Mammal	89	39.2	This study
Reptilia	17	7.5	
<i>Aspidoscelis tigris</i> (17 g)	6	2.6 (50.0)	Grismer, 2002; Klauber, 1972; this study
<i>Aspidoscelis</i> spp. (17 g)	2	0.9 (16.7)	This study
<i>Ctenosaura hemilopha</i> (300 g)	1	0.4 (8.3)	Grismer, 2002.
<i>Sceloporus magister</i> (32 g)	1	0.4 (8.3)	This study
<i>Sceloporus orcutti</i> (32 g)	1	0.4 (8.3)	This study
<i>Sceloporus zosteromus</i> (32 g)	1	0.4 (8.3)	This study
Unidentified Lizard	5	1.8	Klauber, 1972
Totals	227	100.0	

Predator Size Distribution

Dietary items were obtained from 42 juveniles (260–600 mm SVL; 19.2% of sample with prey), 118 adults (610–1180 mm SVL; 53.9% of sample with prey), and 59 of unknown body size (26.9% of sample with prey). Among juveniles with known SVL, one sample was available from a snake <300 mm SVL, four from snakes 300–399 mm, 17 from snakes 400–499 mm, and 15 from snakes 500–599 mm. Among adults, male body length (mean \pm 1 SE: 939 \pm 27 mm SVL; n = 28) averaged 12.9% longer than that of females (832 \pm 29 mm; n = 16), with the difference significant and the effect size large (t = 2.57, df = 42, P = 0.014, 95% CI of difference = 23–191 mm SVL, Cohen's d = 0.81). Adult snakes from coastal populations (904 \pm 17 mm SVL; n = 73) averaged 11.7% larger than those from desert populations (809 \pm 21 mm; n = 41), which was significant (t = 3.49, df = 112, P < 0.001, 95% CI of difference = 41–149 mm SVL, Cohen's d = 0.68).

Ontogenetic Variation

Juvenile (93.3% of 45 specimens) and adult snakes (94.4% of 125 specimens) were equally likely to contain food items (χ^2 = 0.07, df = 1, P = 0.79, ϕ = 0.02). Prey size (excluding multiple prey items), however, was positively associated with predator SVL (r^2 = 0.18, P < 0.001, n = 112; Fig. 4-2). Prey size also differed significantly between the two snake age classes (t = 3.57, df = 119, P = 0.001, 95% CI of difference = 89–311 g, Cohen's d = 0.74), with adult snakes consuming larger prey (mean \pm 1 SE: 268 \pm 32 g; n = 90) than juveniles (68 \pm 20 g; n = 31). This snake age-class difference was probably greater since juveniles were less likely than adults to consume the adult prey

whose mass, derived from the literature, was used for the analysis. Only adult rattlesnakes consumed the largest prey items (western spotted skunk, *Spilogale gracilis*; cottontail rabbit, *Sylvilagus* spp.), including adults of these prey species.

Prey class (analyzed for reptiles and mammals only) was independent of predator age class, with similar proportions of mammals consumed by juvenile (90.7%, $n = 43$) and adult snakes (94.8%, $n = 116$; $\chi^2 = 0.91$, $df = 1$, $P = 0.34$, $\phi = 0.08$). Snakes that ate lizards averaged slightly longer in SVL (864 ± 78 mm SVL, $n = 7$) than those that ate mammals (760 ± 18 mm SVL, $n = 143$), but the difference was not significant ($t = 1.28$, $df = 148$, $P = 0.20$, 95% CI of difference = -57 – 267 mm SVL, Cohen's $d = 0.50$). Among juvenile snakes with identifiable prey and known body size, the one individual <300 mm SVL consumed a rodent, all four individuals 300–399 mm consumed rodents, and 96.9% of 32 individuals 400–599 cm SVL consumed rodents. Thus, both juvenile and adult age classes consumed a near-exclusive mammal diet.

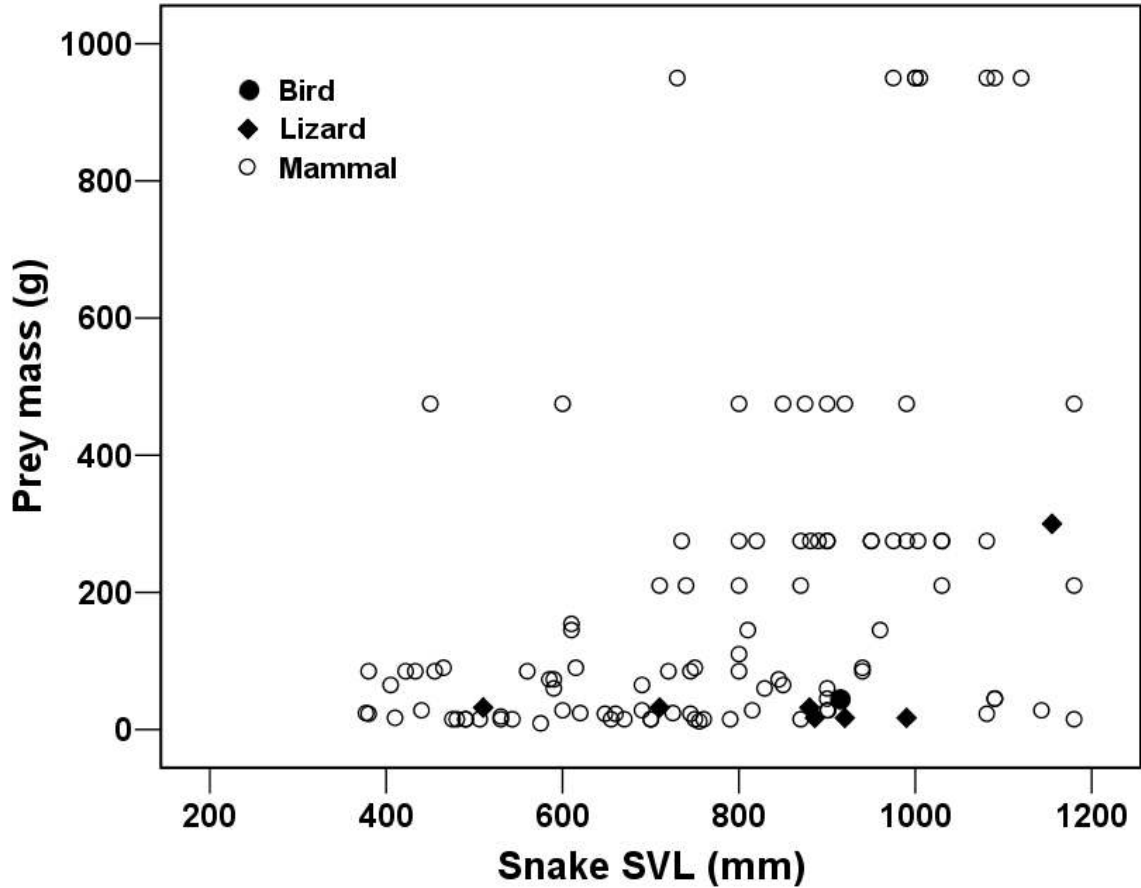


FIG. 4-2.—Predator-prey size relationships for three major food types of the red diamond rattlesnake (*Crotalus ruber*). Note the significant positive relationship between snake length and prey mass, and the consumption primarily of mammals by all size classes of snake.

Sex Differences

Among museum specimens, males (100% of 16 specimens) and females (92,3% of 13 specimens) were equally likely to contain prey items ($\chi^2 = 1.28$, $df = 1$, $P = 0.26$, $\phi = 0.21$). However, the two sexes appeared to consume prey of different sizes. Controlling for body length among the 25 male and 12 female snakes with adequate data, the effect of sex on prey mass was significant (ANCOVA using \log_{10} -transformed prey mass: $F_{1,33} = 6.12$, $P = 0.019$, partial $\eta^2 = 0.16$), with males consuming larger prey items than females

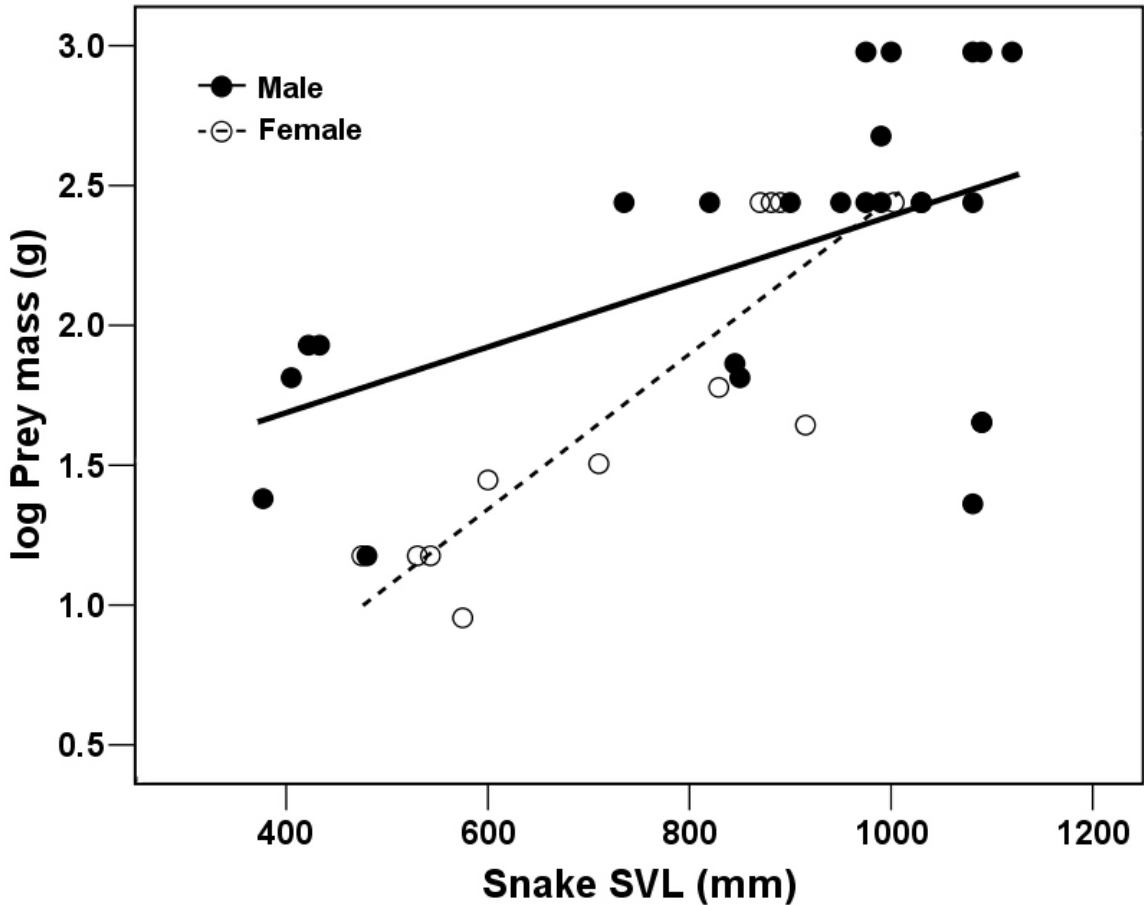


FIG. 4-3.—Comparison of predator-prey size relationships between male and female red diamond rattlesnakes (*Crotalus ruber*). Note the consumption of relatively larger prey by males, particularly when small. Males also attain a larger body size than females.

(Fig. 3). The effect of snake length in this ANCOVA model was also highly significant ($F_{1,33} = 24.92, P < 0.001, \text{partial } \eta^2 = 0.43$). The near-significant interaction between snake length and sex ($F_{1,33} = 4.10, P = 0.051, \text{partial } \eta^2 = 0.11$) suggested that the difference in prey size between sexes was more pronounced for smaller compared to larger snakes (Fig. 3). When we limited analysis only to adult snakes (20 males, 7 females), neither sex ($F_{1,24} = 0.70, P = 0.41, \text{partial } \eta^2 = 0.03$) nor snake length ($F_{1,24} = 0.83, P = 0.37, \text{partial } \eta^2 = 0.03$) remained significant (the non-significant interaction term was removed from the final model). With analysis restricted to the five juveniles of

each sex, statistical power was too low to put confidence in the non-significant ANCOVA effects, but a *t*-test (of log₁₀-transformed mass) confirmed the larger prey mass of juvenile male snakes relative to females (54.8 ± 14.9 g and 16.4 ± 3.1 g, respectively; $t = 2.65$, $df = 8$, $P = 0.029$, 95% CI of difference = 0.06–7.2 g, Cohen's $d = 1.59$).

Geographic Variation

Specimens from coastal (60.6% of 33 specimens) and desert (56.3% of 64 specimens) populations were equally likely to contain prey when analysis was restricted to LACM specimens (for this analysis only) to avoid the aforementioned geographic bias in sampling ($\chi^2 = 0.17$, $df = 1$, $P = 0.68$, $\phi = 0.04$). Prey class, however, was significantly related to predator geographic location, with snakes from coastal populations (1.2% of 82 specimens) consuming lizards less often than those originating from desert localities (9.8% of 92 specimens; $\chi^2 = 5.87$, $df = 1$, $P = 0.015$, $\phi = 0.18$; note the small effect size). Snakes from coastal populations also consumed larger prey (304 ± 39 g) than those from desert locations (103 ± 26 g), even when controlling for body size (ANCOVA using log₁₀-transformed prey mass: $F_{1,105} = 8.86$, $P = 0.004$, partial $\eta^2 = 0.08$; the non-significant interaction term was removed from the final model). Again, the effect of snake size in this ANCOVA model was significant ($F_{1,105} = 7.04$, $P = 0.009$, partial $\eta^2 = 0.06$). We assumed the effects of sex and geographic location were independent, since the ratio of males to females from the two regions was statistically similar ($\chi^2 = 1.05$, $df = 1$, $P = 0.31$, $\phi = 0.16$, $n = 40$; note the small effect size). Because of incomplete data for many individual snakes, the inclusion of both sex and geographic location in the same ANCOVA model would have prohibitively reduced sample size and statistical power.

Seasonal Variation

Food items were identified for all months represented by specimens (February through December; Fig. 4-4), including the winter. Seasonal differences (analyzed for museum specimens only) were compared by month-pairs (pairing was necessary to collapse categories: Mar + Apr, May + Jun, Jul + Aug, Sep + Oct, Nov + Feb) and by season (spring, fall). The presence versus absence of prey was independent of predator collection month-pair ($\chi^2 = 4.33$, $df = 4$, $P = 0.36$, Cramer's $V = 0.18$, $n = 135$) and season ($\chi^2 = 3.32$, $df = 1$, $P = 0.069$, $\phi = 0.16$, $n = 135$), and effect sizes were relatively small. One winter meal was recorded from Baja and five at the northern periphery of the range in California, all involving mammal species ranging in size from *Peromyscus* (45 g) to *Otospermophilus* (475 g) and *Sylvilagus* (950 g). These winter records were all based on fecal samples, although large bulges representing unknown prey species were occasionally observed during winter in radio-tracked snakes.

Prey class consumed appeared to be consistent for the two seasons ($\chi^2 = 0.30$, $df = 1$, $P = 0.58$, $\phi = 0.05$). Mammals comprised the majority of the snake's diet during both the active (95.2% of 145 items) and inactive (100% of six items) seasons. Prey size was also similar for the active (169 ± 23 g, $n = 100$) and inactive seasons (379 ± 216 g, $n = 4$; $t = 1.76$, $df = 102$, $P = 0.082$, 95% CI of difference = -447–27 g, Cohen's $d = 0.90$), but the large effect size suggested that large meals are more often acquired during winter (or that the remains of large meals persist longer in the digestive tract).

Discussion

Our data revealed that *C. ruber* specializes on mammalian prey (91.6% of all prey items), supporting the general consensus of anecdotal reports found in the literature

(Campbell and Lamar, 2004; Klauber, 1972). Terrestrial rodents constituted the primary prey source. Wood rats (*Neotoma* spp., 21.0%) were the most abundant prey species, followed by kangaroo rats (*Dipodomys* spp.), pocket mice (*Chaetodipus* spp.), and deer mice (*Peromyscus* spp.) equally represented in the diet (15.1% for each).

Comparable reliance on mammalian prey bases has been reported for most medium- to large-bodied rattlesnake species, including *C. atrox* (>80%; Beavers, 1976; Reynolds and Scott, 1982; Spencer, 2003), *C. catalinensis* (70.7%; Avila-Villegas et al., 2007), *C. durissus* (>99%; da Graça Salomão et al., 1995; Sant'Anna and Abe, 2007), *C.*

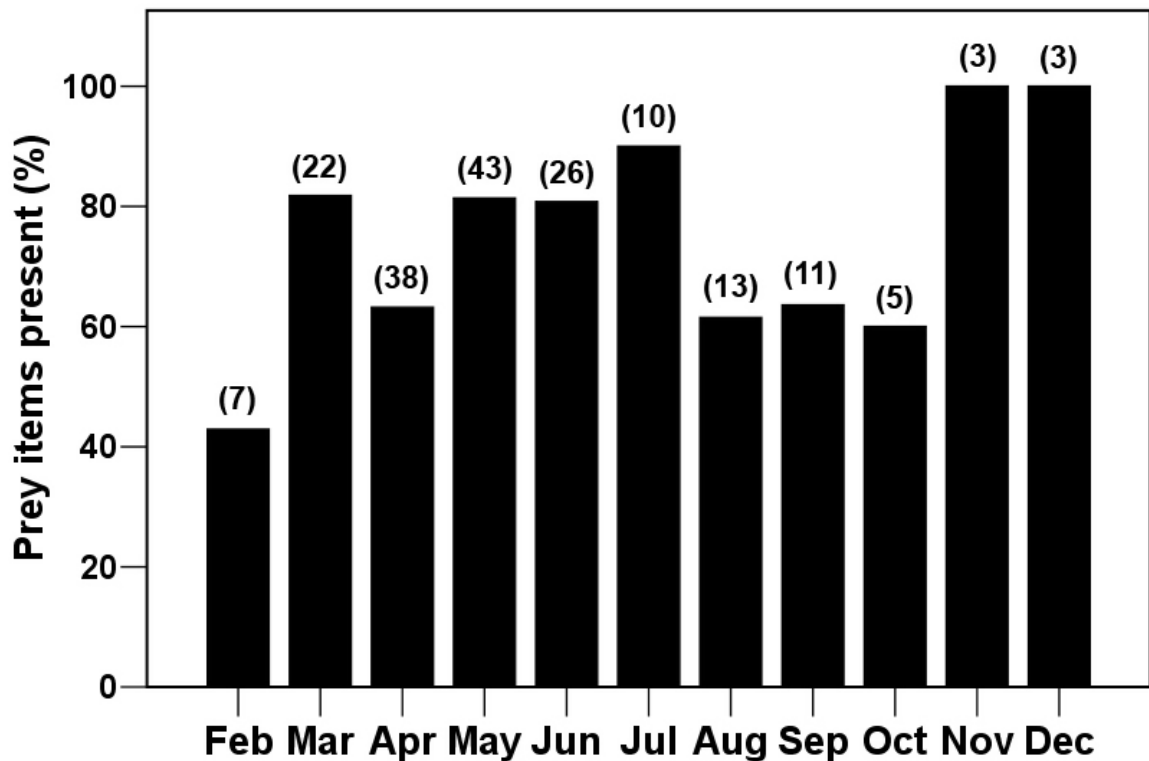


FIG. 4-4.—Percentage of red diamond rattlesnakes (*Crotalus ruber*) containing food items during each month (no data were available for January). Note the consumption of food items year-round.

horridus (95.8%; Clark, 2002), *C. molossus* (83.3%; Reynolds and Scott, 1982), most *C. oreganus* subspecies (>74%; Diller and Johnson, 1988; Diller and Wallace, 1996; Fitch and Twinning, 1946; Glaudas et al., 2008; Labonte, 2008; Macartney, 1989; Mackessy, 1988; Wallace and Diller, 1990; Weaver and Lahti, 2005), *C. viridis abyssus* (82.6%;

Reed and Douglas, 2002), and *C. scutulatus* (>86%; M. D. Cardwell, personal communication; Reynolds and Scott, 1982; but see Salazar and Lieb, 2003). This contrasts with the trend toward greater reliance on ectothermic prey by medium- and small-bodied rattlesnake species, including *C. enyo* (39.7%; Taylor, 2001), *C. lepidus* (ca. 69%; Beaupre, 1995; Holycross et al., 2002a), *C. o. concolor* (up to 64%; Mackessy et al., 2003; Parker and Anderson, 2007), *C. pricei* (>70%; Prival et al., 2002), *C. willardi* (55.8%; Holycross et al., 2002b), and *Sistrurus catenatus* (up to 68.5%; Holycross and Mackessy, 2002; but see Keenlyne and Beer, 1973). However, seasonal, habitat, phylogenetic, and other influences may contribute to or override the effects of body size on dietary tendencies.

Some rattlesnake species exhibit ontogenetic shifts in diet, with juveniles feeding largely on lizards or other ectotherms, and adults transitioning to rodent prey as adults (e.g., Glaudas, et al., 2008; Holycross and Mackessy, 2002; LaBonte, 2008; Mackessy, 1988; Taylor, 2001). Although lizards are occasionally taken by *C. ruber* (cf. Grismer, 2002), we found that lizards represent only a small portion of the diet. Thus, *C. ruber* consumes primarily rodents during all life stages. Although snakes consume increasingly larger prey as they grow, even the largest adults continue to prey on the smallest prey species (Fig. 4-2). Some rattlesnake species drop smaller prey from their diet as they grow (e.g., Glaudas et al., 2008), whereas others do not (e.g., Clark, 2002; Sant'Anna and

Abe, 2007; Weatherhead et al., 2009). Interestingly, the closely-related insular *C. catalinensis* preys on lizards at nearly three times the rate as *C. ruber*; however, rodents still constitute 70.7% of the diet of *C. catalinensis* (Avila-Villegas et al., 2007).

Sexual differences in diet exist among many sexually dimorphic snakes, but in rattlesnakes these differences relate to mere size disparity between males and females (Glaudias et al., 2008), or to frequency of feeding, with gravid females often refraining from meals (Keenlyne, 1972; Klauber, 1972; Prival et al., 2002). Although most snake species exhibit female-larger sexual size dimorphism (Shine, 1991b), the majority of rattlesnakes, particularly larger species, exhibit male-larger sexual size dimorphism (Taylor and DeNardo, 2008). Our data confirmed that adult *C. ruber* males averaged larger than females. Sexual head size dimorphism has also been documented in several rattlesnake species. Females of female-larger *C. cerastes* have relatively larger heads than males (Klauber, 1972), and males of male-larger *C. oreganus lutosus* have relatively larger heads than females (Glaudias et al., 2008). Klauber (1972) looked for but did not detect head size dimorphism in *C. ruber*, so we did not expect to see differences in prey size consumed by males and females of a given body size. When controlling for body length, males appeared to consume larger prey than females, but supplemental analyses confirmed that this sex difference was limited to juveniles only, and could represent an artifact of the small sample size for juveniles. The difference could also have resulted from using adult prey mass for analyses, with the juvenile males eating more young of the larger prey species rather than actually consuming larger prey.

Our data suggest that *C. ruber* exhibits geographic variation in both body size and diet, as coastal snakes averaged longer in body length and consumed a higher proportion

of rodents and prey of proportionally larger body mass than snakes from desert populations. This trend offers tentative support for the diet-alteration hypothesis, which predicts that snakes will be larger when larger types of prey are available (Boback, 2003; Forsman, 1991). Differences in prey consumption presumably reflect differences in prey availability in this opportunistic predator, but we are unaware of data addressing differences in prey availability between coastal and desert locations. The differences in prey mass could also reflect our unavoidable reliance on literature values for adult prey mass. Similar to our findings, adult *C. atrox* in Arizona attain larger body size in cool, moist environments than in warm, dry environments, which contrasts with the general pattern in squamate reptiles but may also relate to prey availability (Amarello et al., 2010). Several rattlesnakes demonstrate geographic variation in diet (Beaupre, 1995; Clark, 2002; Glaudas et al., 2008; Holycross and Mackessy, 2002), whereas others utilize a similar diet throughout their range (Holycross et al., 2002a; Spencer, 2003). Some evidence suggests that geographic variation in diet contributes to adaptive venom variation among rattlesnakes (Gibbs and Mackessy, 2009; Salazar and Lieb, 2003).

Rattlesnakes, like most vipers, rely heavily on ambush tactics (Clark, 2006; Reinert et al., 1984), although they also search for ambush sites and for nests and nestlings. Radio-telemetered *C. ruber* at our Chino Hills study site (coastal population; Dugan et al., 2008) took up ambush positions and localities that unambiguously targeted rodents (i.e., positions adjacent to burrows and runways). Similar observations have been made during video monitoring of hunting *C. ruber* in San Diego County (coastal population; Rulon Clark, personal communication). Foraging tactics used for capturing lizard prey are less well understood for rattlesnakes. If lizard capture similarly involves

ambush, it would be difficult to distinguish tactics used to acquire lizard and rodent prey. Accumulating evidence suggests that rattlesnakes, including *C. ruber*, consume carrion when opportunistically encountered (Devault and Krochmal, 2002). The occasional loss of envenomated prey potentially creates an opportunity for locating carrion and recovery of the lost prey item (Diller, 1990; Hayes, 2008). We found no evidence of carrion ingestion in our data set; however, the only means of confirming it would be through direct observation, which is exceptionally rare,

In contrast to most vipers in temperate regions, *C. ruber* occasionally feeds during the winter months. Collection month and season (active and winter) were not significantly associated with the presence of prey items and feeding. However, the food items in winter from the dietary records were all documented from fecal samples, which may not have represented recently acquired prey. We do not know whether gut contents are completely cleared prior to overwintering, and the remains of large meals (rodent hairs in particular) may persist longer in the gut than those from smaller meals. Nevertheless, we occasionally observed telemetered adult *C. ruber* on the surface digesting large food items during the cool winter months at our Chino Hills field site (Dugan, unpub. data), where mean daily high temperature during the winter is 20 C (compared to 32 C in the summer). Smaller meals, less easily detected, are also likely consumed during winter. Mild winters throughout large portions of the range of *C. ruber* probably facilitate opportunistic winter feedings, as noted in a few other vipers in relatively mild climates (Martin and Means, 2000; Mori et al., 2002). The biological implications of year-round feeding are obvious, presenting snakes in such environs an advantage in terms of resource access and fitness. This advantage should be most

important to females, whose reproduction is severely constrained by energy reserves (Beaupre, 2008; Bonnet et al., 2001; Taylor et al., 2005; Taylor and DeNardo, 2008), and to post-parturient females in particular, which are often in poor body condition.

Beck (1995) estimated that an adult rattlesnake in Arizona needs to consume a cumulative prey mass equivalent to 93% of its own body weight to meet annual energy requirements. Based on this estimation and the body weights of *C. ruber* prey items in Table 1, a 1000 mm adult *C. ruber*, which can be expected to weigh 577 g (Klauber, 1937:42), would require a single adult rabbit (*Sylvilagus*, 795–950 g), two adult ground squirrels (*Otospermophilus*, 475 g), three to four adult wood rats (*Neotoma*, 145–210 g), five to nine adult kangaroo rats (*Dipodomys*, 65–110 g), 12–60 adult mice (*Chaetodipus* or *Peromyscus*, 9–45 g), or some combination of these prey types. A 1250 mm snake weighing 1205 g and a 1500 mm snake weighing 2199 g (Klauber, 1937:42) would require 2.1- and 3.8-fold more prey mass than a 1000 mm individual. Thus, an adult *C. ruber* would clearly benefit by feeding on the largest prey items available, but should consume smaller, presumably more abundant prey as well.

Acknowledgments

K. Beaman, M. Cardwell, A. Figueroa, D. Lohr, B. McGurty, and C. Rodriguez assisted in specimen examination, field work, and/or data collection. Rulon Clark generously shared his unpublished feeding observations. The following provided important field observations: T. Brown, L. L. Grismer, J. Jones, J. Kidd, R. Lovich, M. Noll, and H. Perrine. Brad Hollingsworth supplied measurements of snakes in the SDNHM collection. Research was approved by the Loma Linda University Institutional

Animal Care and Use Committee, and was conducted under permits issued to the senior author by the California Department of Fish and Game and California State Parks.

References

- ARNOLD, S. J. 1997. Foraging theory and prey-size-predator-size relations in snakes. Pp. 87–115. *In* R. A. Seigel, and J. T. Collins (eds), *Snakes: Ecology and Behavior*. McGraw-Hill, New York, New York, USA.
- AVILA-VILLEGAS, H., M. MARTINS, AND G. ARNAUD. 2007. Feeding ecology of the endemic rattleless rattlesnake, *Crotalus catalinensis*, of Santa Catalina Island, Gulf of California, Mexico. *Copeia* 2007:80–84.
- BARLOW, A., C. E. POOK, R. A. HARRISON, AND W. WUSTER. 2009. Co-evolution of diet and prey-specific venom activity supports the role of selection in snake venom evolution. *Proceedings of the Royal Society B* 276:2443–2449.
- BEAMAN, K. R., AND E. A. DUGAN. 2006. *Crotalus ruber* (red diamond rattlesnake). *Catalogue of American Amphibians and Reptiles* 840:1–17.
- BEAUPRE, S. J. 1995. Comparative ecology of the mottled rock rattlesnake, *Crotalus lepidus*, in Big Bend National Park. *Herpetologica* 51:45–56.
- BEAUPRE, S. J. 2008. Annual variation in time-energy allocation by timber rattlesnakes (*Crotalus horridus*) in relation to food acquisition. Pp. 111–122. *In* W. K. Hayes, K. R. Beaman, M. D. Cardwell, and S. P. Bush (eds.), *The Biology of Rattlesnakes*. Loma Linda University Press, Loma Linda, California, USA.
- BEAVERS, R. A. 1976. Food habits of the western diamondback rattlesnake, *Crotalus atrox*, in Texas (*Viperidae*). *Southwestern Naturalist* 20:503–515.
- BECK, D. 1995. Ecology and energetics of three sympatric rattlesnake species in the Sonoran Desert. *Journal of Herpetology* 29:211–223.
- BOBACK, S. M. 2003. Body size evolution in snakes: evidence from island populations. *Copeia* 2003:81–94.
- BONINE, K. E. AND T. GARLAND, JR. 1999. Sprint performance of phrynosomatid lizards, measured on a high-speed treadmill, correlates with hindlimb length. *Journal of Zoology*, 248:255–265.
- BONNET, X., G. NAULLEAU, R. SHINE, AND O. LOURDAIS. 2001. Short-term versus long-term effects of food intake on reproductive output in a viviparous snake, *Vipera aspis*. *Oikos* 92:297–308.
- BROWN, T. K., J. M. LEMM, J.-M. MONTAGNE, AND A. C. ALBERTS. 2008. Spatial ecology, habitat use, and survivorship of resident and translocated red diamond rattlesnakes (*Crotalus ruber*). Pp. 377–394. *In* W. K. Hayes, K. R. Beaman, M. D. Cardwell, and

- S. P. Bush (eds.). The Biology of Rattlesnakes. Loma Linda University Press, Loma Linda, California, USA.
- CAMPBELL, J. A., AND W. W. LAMAR. 2004. Venomous Reptiles of the Western Hemisphere, 2 volumes. Cornell University Press, Ithaca, New York, USA.
- CAROTHERS, J. H. 1983. Size-related activity patterns in a herbivorous lizard. *Oecologia* 57:103–106.
- CLARK, R. W. 2002. Diet of the timber rattlesnake, *Crotalus horridus*. *Journal of Herpetology* 36:494–499.
- CLARK, R. W. 2006. Fixed videography to study predation behavior of an ambush foraging snake, *Crotalus horridus*. *Copeia* 2006:181–187.
- COHEN, J. 1988. Statistical power analysis for the behavioral sciences. 2nd edition. Erlbaum, Hillsdale, New Jersey, USA..
- COSTA, G. C., L. J. VITT, E. R. PIANKA, D. O MESQUITA, AND G. R. COLLI. 2008. Optimal foraging constrains macroecological patterns: body size and dietary niche breadth in lizards. *Global Ecology and Biogeography* 17:670–677.
- CREER, S., W.-H. CHOU, A. MALHOTRA, AND R. S. THORPE. 2002. Offshore insular variation in the diet of the Taiwanese bamboo viper *Trimeresurus stejnegeri* (Schmidt). *Zoological Science* 19:907–913.
- CREER, S., A. MALHOTRA, R. S. THORPE, R. STOCKLIN, P. FAVREAU, AND W.-H. CHOU. 2003. Genetic and ecological correlates of intraspecific variation in pitviper venom composition detected using matrix-assisted laser desorption time-of-flight mass spectrometry (MALDITOF-MS) and isoelectric focusing. *Journal of Molecular Evolution* 56:317–329.
- DA GRAÇA SALOMÃO, M., S. M. A. SANTOS, AND G. PUERTO. 1995. Activity pattern of *Crotalus durissus* (Viperidae, Crotalinae): feeding, reproduction, and snakebite. *Studies on Neotropical Fauna and Environment* 30:101–106.
- DALTRY, J. C., WÜSTER, W. & THORPE, R. S. 1996 Diet and snake venom evolution. *Nature* 379:537–540.
- DARWIN, C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London, UK.
- DEVAULT, T. L., AND A. R. KROCHMAL. 2002. Scavenging by snakes: an examination of the literature. *Herpetologica* 58:429–326.

- DILLER, L. V. 1990. A field observation on the feeding behavior of *Crotalus viridis lutosus*. *Journal of Herpetology* 24:95–97.
- DILLER, L. V. AND D. R. JOHNSON. 1988. Food habits, consumption rates, and predation rates of western rattlesnakes and gopher snakes in southwestern Idaho. *Herpetologica* 44:228–233.
- DILLER, L. V. AND R. L. WALLACE. 1996. Comparative ecology of two snake species (*Crotalus viridis* and *Pituophis melanoleucus*) in southwestern Idaho. *Herpetologica* 52:343–360.
- DUGAN, E. A., A. FIGUEROA, AND W. K. HAYES. 2008. Home range size, movements, and mating phenology of sympatric red diamond (*Crotalus ruber*) and southern Pacific (*C. oreganus helleri*) rattlesnakes in southern California. Pp. 353–364. *In* W. K. Hayes, K. R. Beaman, M. D. Cardwell, and S. P. Bush (eds.), *The Biology of Rattlesnakes*. Loma Linda University Press, Loma Linda, California, USA.
- FIGUEROA, A., E. A. DUGAN, W. K. HAYES. 2008. Behavioral ecology of neonate southern Pacific rattlesnakes (*Crotalus oreganus helleri*) tracked with externally-attached transmitters. Pp. 365–376. *In* W. K. Hayes, K. R. Beaman, M. D. Cardwell, and S. P. Bush (eds.), *The Biology of Rattlesnakes*. Loma Linda University Press, Loma Linda, California, USA.
- FITCH, H. S. 1981. Sexual size differences in reptiles. University of Kansas Publications. Museum of Natural History. Miscellaneous Publication Number 70.
- FITCH, H. S. AND H. TWINNING. 1946. Feeding habits of the Pacific rattlesnake. *Copeia* 1946:64–71.
- FORSMAN, A. 1991. Variation in sexual size dimorphism and maximum body size among adder populations: effects of prey size. *Journal of Animal Ecology* 60:253–267.
- GIBBS, H.L., AND S. P. MACKESSY. 2009. Functional basis of a molecular adaptation: Prey-specific toxic effects of venom from *Sistrurus* rattlesnakes. *Toxicon* 53:672–679.
- GLAUDAS, X., T. JEZKOVA, AND J. A. RODRIGUES-ROBLES. 2008. Feeding ecology of the Great Basin rattlesnake (*Crotalus oreganus lutosus*, Viperidae). *Canadian Journal of Zoology* 86:1–12.
- GOLDBERG, S. R. 1999. Reproduction in the red diamond rattlesnake in California. *California Fish and Game* 85:177–180.
- GREENE, H. W. 1983. Dietary correlates of the origin and radiation of snakes. *American Zoologist* 23:431–441.

- GREENE, H. W. 1993. What's good about good natural history? *Herpetological Natural History* 1:3.
- GREENE, H. W. 1997. Snakes, the evolution of mystery in nature. University of California Press, Berkeley, California, USA.
- GRISMER, L. L. 2002. Amphibians and Reptiles of Baja California including its Pacific Islands and the Islands in the Sea of Cortés. University of California Press, Berkeley, USA.
- HALAMA, K. J., A. J. MALISCH, M. ASPELL, J. T. ROTENBERRY, AND M. F. ALLEN. 2008. Modeling landscape niche characteristics of red diamond rattlesnakes (*Crotalus ruber*): Implications for Biology and Conservation. Pp. 463–472. *In* W. K. Hayes, K. R. Beaman, M. D. Cardwell, and S. P. Bush (eds.), *The Biology of Rattlesnakes*. Loma Linda University Press, Loma Linda, California, USA.
- HARTMANN, M. T., P. A. HARTMANN, S. Z. CECHIN, AND M. MARTINS. 2005. Feeding habits and habitat use in *Bothrops pubescens* (Viperidae, Crotalinae) from Southern Brazil. *Journal of Herpetology* 39:664–667.
- HAYES, W. K. 2008. The snake venom-metering controversy: levels of analysis, assumptions, and evidence. Pp. 191–220. *In* W. K. Hayes, K. R. Beaman, M. D. Cardwell, and S. P. Bush (eds.), *The Biology of Rattlesnakes*. Loma Linda University Press, Loma Linda, California, USA.
- HERBERT, S. S., AND W. K. HAYES. 2008. Venom expenditure by rattlesnakes and killing effectiveness in rodent prey: Do rattlesnakes expend optimal amounts of venom? Pp. 221–228. *In* W. K. Hayes, K. R. Beaman, M. D. Cardwell, and S. P. Bush (eds.), *The Biology of Rattlesnakes*. Loma Linda University Press, Loma Linda, California, USA.
- HOJAT, M., AND G. XU. 2004. A visitor's guide to effect sizes: statistical significance versus practical (clinical) importance of research findings. *Advances in Health Sciences Education: Theory and Practice* 9:241–249.
- HOLYCROSS, A. T. AND S. P. MACKESSY. 2002. Variation in the diet of *Sistrurus catenatus* (massasagua), with emphasis on *Sistrurus catenatus edwardsii* (desert massasagua). *Journal of Herpetology* 36:454–464.
- HOLYCROSS, A. T., C. W. PAINTER, D. B. PRIVAL, D. E. SWANN, M. J. SCHROFF, T. EDWARDS, AND C. R. SCHWALBE. 2002a. Diet of *Crotalus lepidus klauberi* (banded rock rattlesnake). *Journal of Herpetology* 36:589–597.
- HOLYCROSS, A. T., C. W. PAINTER, D. G. BARKER, AND M. E. DOUGLAS. 2002b. Foraging ecology of the threatened New Mexico ridge-nosed rattlesnake (*Crotalus willardi obscurus*). Pp. 243–251. *In* G. W. Schuett, M. Hoggren, M. E. Douglas, and H. W.

- Greene (eds). Biology of the Vipers. Eagle Mountain Publ., Eagle Mountain, Utah, USA
- JADIN, R. C. 2007. Prey items of the Tzotzil montane pitviper (*Cerrophidion tzotzilorum*). Southwestern Naturalist 52:437–438.
- JAMESON, E. W., JR., AND H. J. PEETERS. 1988. Mammals of California. University of California Press, Berkeley, USA.
- JENNINGS, M. R., AND M. P. HAYES. 1994. Amphibian and Reptile Species of Special Concern in California. California Department of Fish and Game, Rancho Cordova, California, USA.
- KEENLYNE, K. D. 1972. Sexual differences in feeding habits of *Crotalus horridus horridus*. Journal of Herpetology 6:234–237.
- KEENLYNE, K. D. AND J. D. BEER. 1973. Food habits of *Sistrurus catenatus catenatus*. Journal of Herpetology 4:381–382.
- KLAUBER, L. M. 1937. A statistical study of the rattlesnakes: IV. The growth of the rattlesnake. Occasional Papers of the San Diego Natural History Society 3:1–56.
- KLAUBER, L. M. 1972. Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind. 2nd ed. 2 vol. University of California Press, Berkeley, USA.
- LABONTE, J. P. 2008. Ontogeny of prey preference in the southern Pacific rattlesnake, *Crotalus oreganus helleri*. Pp. 169–174. In W. K. Hayes, K. R. Beaman, M. D. Cardwell, and S. P. Bush (eds.). The Biology of Rattlesnakes. Loma Linda University Press, Loma Linda, California, USA.
- LEVITON, A. E., R. H. GIBBS JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology. Part 1. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985:802–832.
- LEWIS, D. S., R. VAN VEEN, AND B. S. WILSON. 2010. Conservation implications of small Indian mongoose (*Herpestes auropunctatus*) predation in a hotspot within a hotspot: the Hellshire Hills, Jamaica. Biological Invasions 13:25–33.
- LILLYWHITE, H. B., C. M. SHEEHY III, AND F. ZAIDEN III. 2008. Pitviper scavenging at the intertidal zone: an evolutionary scenario for invasion of the sea. Bioscience 58:947–955.
- LUISELLI, L. 2006. Food niche overlap between sympatric potential competitors increases with habitat alteration at different trophic levels in rain-forest reptiles (omnivorous tortoises and carnivorous vipers). Journal of Tropical Ecology 22:695–704.

- MACARTNEY, J. M. 1989. Diet of the northern Pacific rattlesnake, *Crotalus viridis oregonus*, in British Columbia. *Herpetologica* 45:299–304.
- MACKESSY, S. P. 1988. Venom ontogeny in the Pacific rattlesnakes *Crotalus viridis helleri* and *C. v. oregonus*. *Copeia* 1988:92–101.
- MACKESSY, S. P., K. WILLIAMS, AND K. G. ASHTON. 2003. Ontogenetic variation in venom composition and diet of *Crotalus oregonus concolor*: A case of venom paedomorphosis? *Copeia* 2003:769–782.
- MARTIN, W. H. AND D. B. MEANS. 2000. Distribution and habitat relationships of the eastern diamondback rattlesnake (*Crotalus adamanteus*). *Herpetological Natural History* 7:9–34.
- MARTINS, M., M. S. ARAUJO, R. J. SAWAYA, AND R. NUNES. 2001. Diversity and evolution of macrohabitat use, body size and morphology in a monophyletic group of neotropical pitvipers (*Bothrops*). *Journal of Zoology* 254:529–538,
- MOORE, T. D., L. E. SPENCE, C. E. DUGNOLLE, AND W. G. HEPWORTH. 1974. Identification of the dorsal guard hairs of some mammals of Wyoming. Wyoming Fish and Game Department, Cheyenne, Wyoming, USA.
- MORI, A., M. TODA, AND H. OTA. 2002. Winter activity of the hime-habu (*Ovophis okinavensis*) in the humid subtropics: foraging on breeding anurans at low temperatures. In G. W. Schuett, M. Hoggren, M. E. Douglas, and H. W. Greene (eds). *Biology of the Vipers*. Eagle Mountain Publ., Eagle Mountain, Utah, USA.
- NAKAGAWA, S. 2004. A farewell to Bonferroni: The problems of low statistical power and publication bias. *Behavioral Ecology* 15:1044–1045.
- NOSS, R. F. AND R. L. PETERS. 1995. Endangered ecosystems. A status report on America's vanishing habitat and wildlife. Defenders of Wildlife, Washington, D.C.
- PARKER J. M. AND S. H ANDERSON. 2007. Ecology and behavior of the midget faded rattlesnake (*Crotalus oregonus concolor*) in Wyoming. *Journal of Herpetology* 41:45–51.
- PATTEN, R. B. AND B. H. BANTA. 1980. A rattlesnake, *Crotalus ruber*, feeds on a road killed animal. *Journal of Herpetology* 14:111–112.
- PLEGUEZUELOS, J. M., J. R. FERNÁNDEZ-CARDENETE, S. HONRUBIA, M. FERICHE, AND C. VILAFRANCA. 2007. Correlates between morphology, diet and foraging mode in the ladder snake *Rhinechis scalaris* (Schinz, 1822). *Contributions to Zoology* 76:179–186.

- PRIVAL, D. B., M. J. GOODE, D. E. SWANN, C. R. SCHWALBE, AND M. J. SCHROFF. 2002. Natural history of a northern population of twin-spotted rattlesnakes, *Crotalus pricei*. *Journal of Herpetology* 36:598–607.
- REED, R. N., AND M. E. DOUGLAS. 2002. Ecology of the Grand Canyon rattlesnake (*Crotalus viridis abyssus*) in the Little Colorado River Canyon, Arizona. *Southwestern Naturalist* 47:30–39.
- REINERT, H. K., D. CUNDALL, AND L. M. BUSHAR. 1984. Foraging behavior of the timber rattlesnake, *Crotalus horridus*. *Copeia* 1984:976–981.
- REYNOLDS R. P. AND N. J. SCOTT, JR. 1982. Use of a mammalian resource by a Chihuahuan snake community. Pp. 99–118. *In* N. J. Scott, Jr. (Ed.), *Herpetological Communities*. U.S. Fish and Wildlife Service. Wildlife Research Report 13.
- RODRIGUEZ-ROBLES, J. A., C. J. BELL, AND H. W. GREENE. 1999. Gape size and evolution of diet in snakes: feeding ecology of erycine boas. *Journal of Zoology* 248:49–58.
- SALAZAR, J. D., AND C. S. LIEB. 2003. Geographic diet variation of Mojave rattlesnake (*Crotalus scutulatus*). Undergraduate Thesis, Border Bridges to the Baccalaureate Program, University of Texas at El Paso and El Paso Community College, USA. <http://bridges.utep.edu/2003%20Students/Salazar,%20Jennifer/Salazar,%20Jennifer.pdf>
- SANT'ANNA, S. S., AND A. S. ABE. 2007. Diet of the rattlesnake *Crotalus durissus* in southeastern Brazil (Serpentes, Viperidae). *Studies on Neotropical Fauna and Environment* 42:169–174.
- SAVIOZZI, P., M. A. L. ZUFFI. 1997. An integrated approach to the study of the diet of *Vipera aspis*. *Herpetological Review* 28:23–24.
- SCHOENHERR, A. A. 1992. *A natural history of California*. University of California Press. Berkeley, California, USA.
- SHINE, R. 1991a. Why do larger snakes eat larger prey items? *Functional Ecology* 5:493–502.
- SHINE, R. 1991b. Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. *American Naturalist* 138: 103–122.
- SHINE, R., AND X. BONNET. 2000. Snakes: a new "model organism" in ecological research? *Trends in Ecology and Evolution* 15:221–222.
- SHINE, R., AND S. LI-XIN. 2002. Arboreal ambush site selection by pit-vipers *Gloydius shedaoensis*. *Animal Behavior* 63:565–576.

- SIBLEY, D. A. 2000. National Audubon Society The Sibley Guide to Birds. Chanticleer Press, Inc., New York, New York, USA.
- SPENCER, C. L. 2003. Geographic variation in the morphology, diet, and reproduction of a widespread pitviper, *Crotalus atrox*. Unpublished Dissertation. University of Texas at Arlington, USA.
- STEBBINS, R. C. 1985. A field guide to western reptiles and amphibians. 2nd revised edition. Houghton Mifflin Company, Boston, Massachusetts, USA.
- TAYLOR, E. N. 2001. Diet of the Baja California rattlesnake, *Crotalus enyo* (Viperidae). *Copeia* 2001:553–555.
- TAYLOR, E. N., AND D. F. DENARDO. 2008. Proximate determinants of sexual size dimorphism in the western diamond-backed rattlesnake (*Crotalus atrox*). Pp. 91–100. *In* W. K. Hayes, K. R. Beaman, M. D. Cardwell, and S. P. Bush (eds.), *The Biology of Rattlesnakes*. Loma Linda University Press, Loma Linda, California, USA.
- TAYLOR, E. N., M. A. MALAWY, D. M. BROWNING, S. V. LEMAR, AND D. F. DENARDO. 2005. Effects of food supplementation on the physiological ecology of female western diamond-backed rattlesnakes (*Crotalus atrox*). *Oecologia* 144:206–213.
- TEVIS, L. JR. 1943. Field notes on a red diamond rattlesnake in lower California. *Copeia* 1943: 242–245.
- VINCENT, S. E., A. HERREL, AND D. J. IRSCHICK. 2004. Sexual dimorphism in head shape and diet in the cottonmouth snake (*Agkistrodon piscivorus*). *Journal of Zoology* 264:53–59.
- VINCENT, S. E., M. C. BRANDLEY, A. HERREL, AND M. E. ALFARO. 2009. Convergence in trophic morphology and feeding performance among piscivorous natricine snakes. *Journal of Evolutionary Biology* 22:1203–1211.
- WALLACE R. L. AND L. V. DILLER. 1990. Feeding ecology of the rattlesnake, *Crotalus viridis oregonus*, in northern Idaho. *Journal of Herpetology* 24:246–253.
- WEATHERHEAD, P. J., J. M. KNOX, D. S. HARVEY, D. WYNN, J. CHIUCCHI, AND H. L. GIBBS. 2009. Diet of *Sistrurus catenatus* in Ontario and Ohio: Effects of body size and habitat. *Journal of Herpetology* 43:693–697.
- WEAVER, R. E., AND M. E. LAHTI. 2005. Diet of the northern Pacific Rattlesnake (*Crotalus viridis oregonus*) in the Yakima River Canyon of central Washington state. Pg. 51 in W. K. Hayes (ed.), *Program and Abstracts of the Biology of the Rattlesnakes Symposium*. Loma Linda University, Loma Linda, California, USA.

- WONG, H. 1997. Comments on the snake records of *Chilomeniscus cinctus*, *Crotalus exsul*, and *C. mitchellii* from Islas Magdalena and Santa Margarita. *Herpetological Review* 28:188–189.
- ZAR, J. H. 1996. *Biostatistical Analysis*, 3rd ed. Prentice Hall, Englewood Cliffs, New Jersey, USA.
- ZELANIS, A., S. R. TRAVAGLIA-CARDOSO, AND M. D.F. D FURTADO. 2008. Ontogenetic changes in the venom of *Bothrops insularis* (Serpentes: Viperidae) and its biological implication. *South American Journal of Herpetology* 3:43–50.

Appendix

Specimens Examined

Crotalus ruber: ABDSP 4211, 4214, 4216, 4224, 4263, 4295. LACM 2965, 3037, 3038, 3039, 3040, 3041, 3042, 3044, 3047, 3051, 3052, 3053, 3054, 3055, 3056, 20008, 20011, 20014, 20015, 20016, 20018, 20019, 20020, 25079, 25080, 28020, 28021, 28022, 28023, 51860, 52559, 52560, 52561, 52562, 52563, 63445, 76290, 76291, 104997, 104998, 104999, 105000, 105001, 105002, 105003, 105004, 105005, 105006, 105007, 105008, 105009, 105010, 105011, 105012, 105013, 105014, 105015, 105016, 105017, 105018, 105019, 105020, 105021, 105022, 105023, 105024, 105025, 105026, 105027, 105028, 105029, 105030, 105032, 105033, 105034, 105035, 105036, 105037, 105038, 105039, 105041, 105042, 105043, 105044, 105045, 105046, 105047, 105053, 105054, 116019, 116020, 116021, 116022, 116023, 122109, 122110, 125999, 126080, 126225, 128280, 134041, 143738, 143739, 146112, 146129, 152326, 152522, 152525, 152527, 152528. SDNHM 2265, 2695, 17594, 18060, 18732, 20043, 28371, 31328, 31329, 31330, 32536, 32654, 32834, 32845, 33229, 33251, 33341, 33808, 34506, 35764, 35877, 36058, 36059, 36168, 36667, 37633, 38183, 38930, 43548.

CHAPTER FIVE

CONCLUSIONS AND DISCUSSION

In this dissertation, I examined resource use by two sympatric rattlesnake species (*Crotalus ruber* and *C. o. helleri*) within the context of niche partitioning. My efforts represent the most extensive examination of resource use that has been conducted on North American viperids. In this chapter, I will touch on the primary conclusions from each of my studies.

In **Chapter 2**, I assessed potential interspecific differences in two measures of movement ecology and space use: mean daily movement and home range size. In addition, I compared data on the reproductive ecology of each species.

Considering these two measurements of space use, *C. ruber* proved to be largely sedentary when compared to *C. o. helleri*. On average, the home range size of *C. o. helleri* was two- to five-fold larger than that of *C. ruber*. Similarly, *C. o. helleri* exhibited mean daily movements two-fold greater than *C. ruber*. Reproductive ecology of the two species differed dramatically as well. I observed a unimodal mating season (exclusively in spring) in *C. ruber*, whereas *C. o. helleri* exhibited a bi-modal mating season (spring and late summer/fall). Because male rattlesnakes exhibit prolonged mate searching, the observed variation in mating phenology indirectly results in partitioning of temporal resources in the fall. Thus, this chapter suggests the partitioning of resources along the spatial and temporal axes.

In *Chapter 3*, I provided the single most extensive examination of comparative resource use among sympatric North American vipers to date. I compared *C. ruber* and *C. o. helleri* along all four major niche axes (space, temporal, diet, thermal) using radio-telemetry and mark-recapture data collected from my Chino Hills State Park study site. Spatial resources were analyzed in terms of both macrohabitat and microhabitat.

Compositional analysis and logistic regression revealed that *C. ruber* and *C. o. helleri* used different macrohabitats throughout the year (both active and winter seasons). Analysis of microhabitat use relative to the ground surface (above-ground, below ground, arboreal) detected no species differences, with neither species using arboreal habitats often. Thus, niche overlap indices (Pianka's and Czekanowski's) confirmed that macrohabitat overlap was narrow between the species, and microhabitat overlap was broad.

Thermal resource use of microhabitats also differed significantly, with *C. ruber* occupying microhabitats with significantly warmer ground temperature than those occupied by *C. o. helleri*. Similarly, *C. ruber* was observed with significantly greater body-exposure to the sun (i.e., regional heterothermy). However, the niche overlap indices indicated that thermal resource overlap was very broad.

Behavior and seasonality of movements also differed significantly between the two species. In terms of movements, both species were more active during the spring than in other seasons. *Crotalus o. helleri* exhibited higher levels of activity than *C. ruber* in all three seasons, with *C. o. helleri* engaging in locomotion 1.7-fold more often and sexual activities 2.3-fold more frequently than *C. ruber*. However, the patterns of usage were similar, with the indices indicating broad overlap in temporal use of resources.

Diet composition differed significantly between *C. ruber* and *C. o. helleri*, but the differences reflected the prey types that occurred within their preferred macrohabitats. I identified 21 mammal items representing six genera in the exclusively mammalian diet of *C. ruber*, with wood rats (*Neotoma* spp.), which prefer the same cactus habitats as *C. ruber*, representing the most common prey item. The diet of *C. o. helleri* included 30 mammal items distributed across 9 genera and a single lizard species, with pocket mice (*Chaetodipus* spp.) and California ground squirrels (*Otospermophilus beecheyi*), which occupy the same grassland habitats preferred by *C. o. helleri*, being the most common prey recorded. Prey size class also differed between the two snake species. *Crotalus ruber* most often procured medium-sized prey species, whereas *C. o. helleri* most frequently consumed small prey species. Niche overlap indices revealed narrow overlap in diet, more so for prey type than prey size. However, because both species appear to be opportunistic predators, consuming a broad range of prey types, I concluded that dietary differences likely reflected the habitat-specific prey distribution among the different macrohabitats potentially partitioned by the snakes. Thus, this study underscores the difficulty in deciphering niche partitioning when niche axes covary, as can happen with spatial and trophic resources.

To determine whether niche overlap values were significantly less than expected by chance, I subjected them to null models and Monte Carlo simulations. The only evidence for niche partitioning between the two snake species was in prey size, for which observed index values were significantly less than expected in the null model pseudo-communities. Again, these differences could relate to habitat-specific prey distribution among the different macrohabitats potentially partitioned by the snakes. Index values for

temperature were also greater than expected, suggesting that abiotic constraints impose similarity in thermal niche use by the two species.

I conclude that niche separation between these two rattlesnake taxa has probably resulted largely from non-competitive mechanisms. If niche partitioning exists, I believe it occurs subtly along more than one niche axis, but probably more so via differential habitat use than other axes. I suggest that dietary differences reflect habitat preference and body size-dependent differences between the two snake species. Although these sympatric rattlesnakes may be similar to other vipers and most vertebrates in partitioning habitat (Luiselli, 2006a,b; Luiselli et al., 2007), the evidence for demonstrating this remains elusive.

In *Chapter 4*, I provided a detailed description of the diet of the red diamond rattlesnake (*C. ruber*) based on museum specimens, fecal samples from live specimens at my study site, opportunistic field observations, published accounts, and data collected from road-killed specimens. This rangewide description allowed for comparison to a prior study of diet in *C. o. helleri*. Dietary data for *C. ruber* were collected from across the species' range, including southern California (USA) and Baja Norte and Baja Sur (Mexico). The diet of *C. ruber* consisted primarily of mammals in all age classes, although it also included lizards and birds to a lesser extent. Interestingly, *C. ruber* did not exhibit an ontogenetic shift in diet from ectothermic prey (primarily lizards) to endothermic prey (primarily rodents), as has been noted for many other rattlesnake species (Glaudas et al., 2008), including sympatric *C. o. helleri* (Mackessy, 1988). Males consumed larger prey than females, even when controlling for male-larger dimorphism in body size, and adult snakes fed on larger prey than juveniles. Snakes from coastal

populations, which averaged larger than those from desert populations, consumed a higher proportion of rodents, as well as larger prey species, compared to those from the desert. The presence of prey was independent of snake collection month, indicating year-round feeding, even at the northern part of the range. In general, *C. ruber* is an ambush predator of mammalian prey, relying to a lesser extent on lizards, birds, and scavenging to meet annual food resource requirements.

Collectively, these studies add much to our understanding of viper ecology, and build a much-needed data base for two snake species that increasingly conflict with human population growth in southern California.

REFERENCES

- GLAUDAS, X., T. JEZKOVA, AND J. A. RODRIGUES-ROBLES. 2008. Feeding ecology of the Great Basin rattlesnake (*Crotalus oreganus lutosus*, Viperidae). *Canadian Journal of Zoology* 86:1–12.
- LUISELLI, L. 2006a. Resource partitioning and interspecific competition in snakes: The search for general geographical and guild patterns. *Oikos* 114:193–211.
- LUISELLI, L. 2006b. Food niche overlap between sympatric potential competitors increases with habitat alteration at different trophic levels in rain-forest reptiles (omnivorous tortoises and carnivorous vipers). *Journal of Tropical Ecology* 22:695–704.
- LUISELLI, L., E. FILIPPI, AND E. DI LENA. 2007. Ecological relationships between sympatric *Vipera aspis* and *Vipera ursinii* in high-altitude habitats of Central Italy. *Journal of Herpetology* 41:378–384.
- MACKESSY, S. P. 1988. Venom ontogeny in the Pacific rattlesnakes *Crotalus viridis helleri* and *C. v. oreganus*. *Copeia* 1988:92–101.